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THE BOGS OF NORTHERN LOWER MICHIGAN*

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INTRODUCTION

The present paper is one of a series based on the author's detailed studies during the past three decades while at the Biological Station of the University of Michigan.

LOCATION

The region studied (see map, Fig. 1) is located in Emmet and Cheboygan counties, centering around Douglas Lake, a small body of water in the west central part of Cheboygan County at the northern end of the lower peninsula of Michigan, midway between Lake Michigan and Lake Huron, at an elevation of about 710 feet (217 meters) above sea level. The bog part of the region belongs to the Canadian part of the boreal zone, according to Merriam (1898) although the region as a whole partakes of transition zone characteristics as well.

From the phytogeographic standpoint, the vegetation of the region which is located in the transition zone between the northeastern coniferous forest province and the central or deciduous forest province appears in checkerboard array. Although near the northern part of the transition zone, conditions are apparently becoming more favorable to the deciduous forests. Still it is a region of relatively low plant development, as shown by the moisture-temperature index of 3,300 calculated for Alpena, a short distance south (Livingston 1916).

FACTORS

The general factors operating in the Douglas Lake region have been for centuries favorable to the development of trees as a ground cover in the whole region. The temperature is moderate, the rainfall, although moderate, is amply distributed throughout the year. Snow is usually abundant and remains on the ground for a long time. Evaporation in the region is moderate in amount, especially so in the bogs (Gates 1917, 1926).

The climatic conditions most closely resemble those of the Weather Bureau station at Cheboygan, Michigan, a summary of which is given in Table 1. Detailed statistics of the meteorology at the Biological Station during the summer months are given in several papers by the author (Gates 1924, 1930, 1937) and are summarized in Table 2.

The mineral soil is entirely of glacial origin and is prevailingly of a sandy type, but may be mixed with gravel or clayey material in the glacial moraines.

TABLE 1. Meteorological summary, Cheboygan, Michigan. (U. S. Weather Bureau figures.)

Temperature (Degrees F.)	January	February	March	April	May	June	July	August	September	October	November	December
Absolute Maximum	59	51	72	86	89	95	103	95	95	89	73	59
Mean	19	16	25	39	50	61	68	65	60	48	35	23
Absolute Minimum	−20	−38	−22	− 2	17	28	33	35	25	15	− 6	−18
Growing Season (138 days)	...	...	...	...	18	15	...	...	10	3	...	...
Wind	NW	NW	NW	NW	NW	NW	NW	NW	SW	SW	NW	SW
Precipitation (inches)	1.61	1.40	1.77	1.98	2.81	2.66	2.56	2.87	3.25	2.88	2.38	1.68
Total	...	...	...	...	...	...	...	...	...	...	...	27.85
Number of days with precipitation	9	7	6	7	8	7	8	9	8	8	9	9
Total	...	...	...	...	...	...	...	...	...	...	...	95
Snowfall (inches)	15.6	13.6	9.0	2.3	0.7	...	...	...	T	0.7	6.6	12
Total	...	...	...	...	...	...	...	...	...	...	...	62.0

TABLE 2. Meteorological averages, 1912-41, Douglas Lake, Michigan.

Periods		Temperature in degrees F.							Precipitation in inches			Evaporation Dragoyle reading (Beats per minute)*		
	Year of record	Absolute maximum	Absolute minimum	Average maximum	Average minimum	Mean	Solar maximum absolute	Solar maximum average	Precipitation	Days precipitation	Maximum precipitation in one day	6:30 A.M.	Noon	6:00 P.M.
June														
1–6	..	84	28	...	...	...	...	...	...	...	...	...	...	...
7–12	7	96	38	76.4	52.9	64.7	...	...	0.60	1.6	1.20†	...	...	...
13–18	10	93	34	76.1	50.4	63.3	152	131	0.77	1.3	2.24	...	...	...
19–24	20	95	36	75.9	52.1	64.0	159	130	0.39	1.5	1.48	7	49	47
25–30	26	98	30	76.7	53.8	65.3	161	139	0.52	1.8	1.64	12	58	55
Average or extremes	..	98	28	...	...	...	161	...	2.29+	6.3+	2.24	...	...	...
July														
1–6	30	102	38	79.6	54.2	66.9	159	142	0.36	1.4	1.00	14	67	61
7–12	30	102	39	80.2	57.0	68.6	159	142	0.50	1.9	1.73	14	63	63
13–18	30	103	42	80.0	56.6	68.3	156	143	0.47	1.8	1.50	17	62	67
19–24	30	100	40	81.4	57.5	69.4	163	145	0.53	1.7	1.36	14	62	60
25–31	30	104	40	81.0	58.2	69.6	160	143	0.47	1.9	1.15	13	66	60
Average or extremes	..	104	38	80.5	56.8	68.6	163	143	2.34	8.6	1.73	14	64	62
August														
1–6	30	99	36	79.0	56.9	67.9	160	139	0.57	1.6	1.97	13	62	59
7–12	30	98	38	78.5	56.9	67.7	165	142	0.65	2.1	2.20	10	55	52
13–18	30	97	40	78.0	55.9	67.0	157	140	0.51	1.5	1.28	12	62	56
19–24	28	97	39	75.1	54.5	64.8	161	137	0.67	1.7	1.94	8	49	48
25–31	21	91	37	74.5	54.0	64.3	156	133	0.59	1.6	1.92†	...	...	...
Average or extremes	..	99	36	77.3	55.8	66.6	165	138	2.98	8.4	2.20	11	59	54

*Each beat is equivalent to the evaporation of 0.0006081 cc. of water. (Based on 11 years of record.) †Two days.

The actual average atmospheric pressure (Paulin system barometer, 1931-1941) for July is 29.34 inches (993.7 millebars) and for August is 29.39 inches (995.3 millebars).

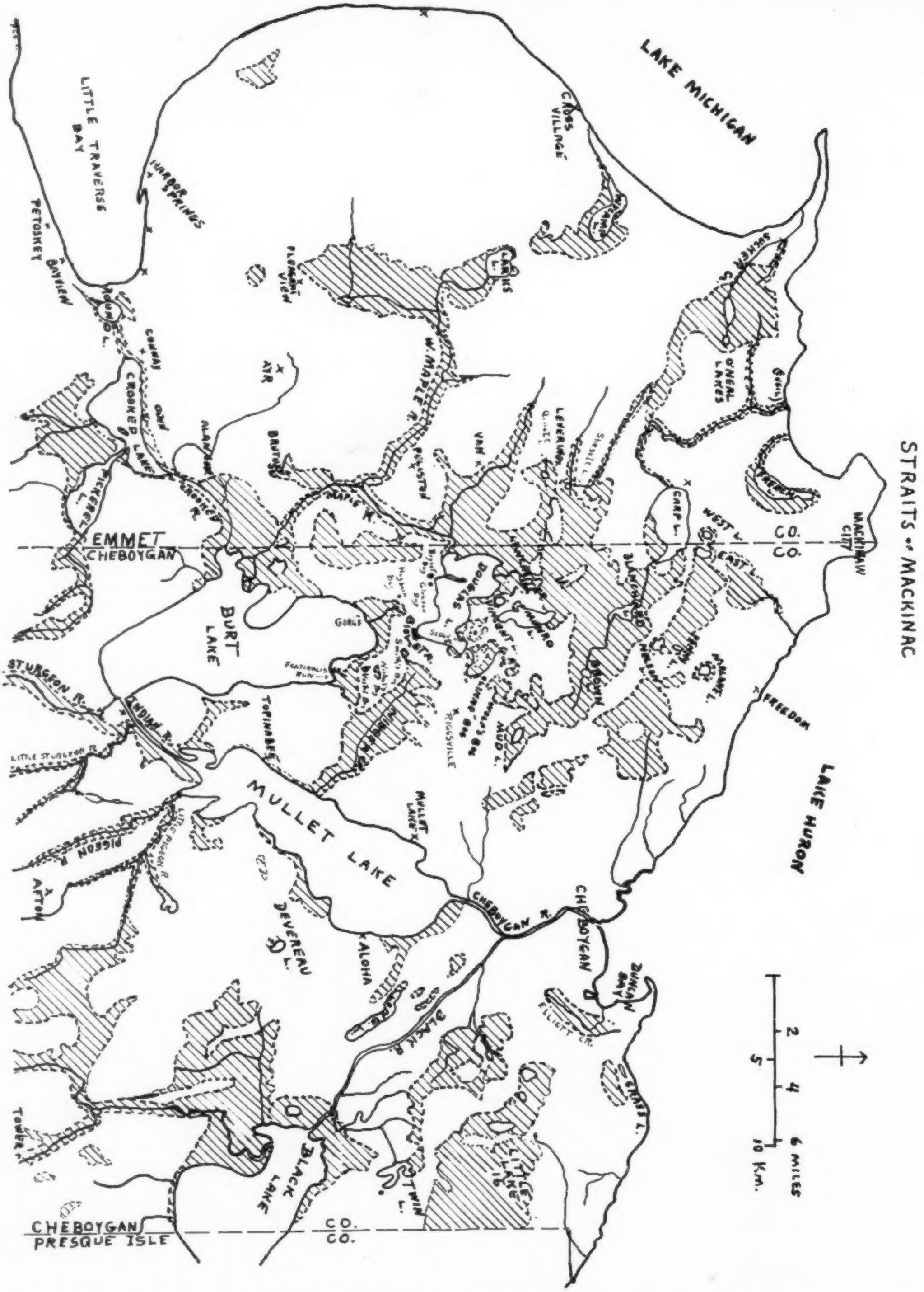


FIG. 1. Sketch map of the northern parts of Emmet and Cheybogan Counties, Michigan, showing the approximate locations of the major areas of bogland indicated by diagonal ruling.

Fire has been a most important factor in the region in recent times, during which fires have been both extensive and of frequent occurrence.

Under the climatic conditions obtaining, the irregular depressions left in the glacial drift, in which water is held, are admirably adapted to the development of bogs. The ample precipitation, well distributed throughout the year, supplies plenty of water at all times. The original soil has little effect on bog development. Fire, on the other hand, modifies, retards, or prevents some expressions of bog character, but fire can seldom prevent some sort of bog development in situations suitable for bogs.

WHERE BOGS DEVELOP

Bogs may be initiated in any sort of a depression or in lowlands. Beach pools may develop into either strictly aquatic situations or, if the proper plants come in, into shallow bogs. Bogs may develop in kettle holes in glacial moraines or in low spots in the upland. Bogs may also develop in quiet bays of lakes, or quiet places in stream channels.

HISTORY OF VEGETATION

Following withdrawal of the ice of the late Wisconsin glaciers, the different parts of the region became vegetated, until at the time of lumbering in the 1870's the uplands were either pine or maple-beech forests, while the lowlands were cedar bogs, a bog developmental stage, or marshes in depressions or along streams. With the lumbermen came removal of the forest, including that from the bogs. Such areas were usually burned and often reburned. The moisture in such areas, however, mitigated the severest effects of fire.

DEFINITION OF BOG

In view of the diversity of opinion in stating the definition of a bog, the following definition is used in this paper, recognizing, however, that bogs and swamps intergrade and no hard and fast line can be drawn between them in all situations in the field.

A bog is an area of vegetation, developing in undrained or poorly drained situations, which by the development of a mat invading open water, forms a cover over a body of water. It consists of a series of successional stages or associations beginning with mat-forming sedges and passing through shrub (mostly ericad) and Sphagnum stages to an expected culmination in the development of a characteristic coniferous tree association.

The term bog thus includes pre-eminently a type of vegetation which controls a habitat and changes the habitat, in the course of its development, from an open area of water to a mat and then to a grounded mat and finally to dry land. One regularly associates lack of circulation of the water with deficient oxygenation and slow decay. The water of bog lakes may be either acid or alkaline but the water in the various plant zones in this region is acid, strongly so in the Sphagnum zone and becoming less so as the Thuja or climax tree stage is reached. The plants in bogs grow slowly. There is a dearth of minerals. The water is cold, especially under the mat, but on hot days the surface of the mat may become hot. These conditions favor peat formation, in fact a bog may be defined as an area vegetated by a flora in which peat-forming types of plants (including certain herbaceous, ericaceous shrubs and coniferous trees) are particularly abundant.

The word swamp is often used to cover at least a part of a bog, as defined above, but had best be kept to designate areas better drained, and without mats developing out over the water. Muskeg is largely synonymous with bog, but is used more to the north.[1]

Under conditions of moist cool climate, bogs may be built up by a Sphagnum ring on uplands. Such bogs, common enough in parts of Europe and occurring in eastern North America, known as raised or upland bogs or hochmoors, are not found under the climatic conditions obtaining in the Douglas Lake region. All of the bogs in this region are of the lowland or flachmoor type.

DEVELOPMENT OF A BOG

A bog normally begins as an open body of water in a depression not so large that wave action can be too serious a factor in hindering development, or in somewhat protected bays of larger bodies of water. The water may be acid or alkaline in reaction, and it may be shallow or deep.

The first plants to appear may do so both in the water and along the shore. In the water there is little difference between the aquatic types of early bog stages or of those of the ordinary aquatic flora of lakes. If the depression is not too deep, attached submerged forms, as Chara, may appear. More frequently, however, in this region the Potamogeton association is usually the first to appear. The Nuphar-Nymphaea association normally follows. Its plants are rooted on the bottom and project up through the water to the surface, upon which the leaves float. If the bottom slopes abruptly downward, this vegetation is limited to a narrow zone. In a shallow basin, this zone may be wide.

Meanwhile the type of vegetation which develops along the shore determines the fate of the area. Associations of *Scirpus validus* or of *Scirpus americanus* or similar types are more likely to be followed by marshes or wooded swamps than by bogs. The initiation of a bog on the other hand requires the establishment of a sufficient number of plants of

[1] For a discussion of the terms: bog, swamp and marsh, see also R. M. Harper in Torrey Bot. Club Bul. **45**: 23-42, 1918 and Wm. N. Clute in Amer. Bot. **36**: 48-49, 1930; **37**: 18, 1931. For a discussion of the structure and development of the association and the basic fundamentals of vegetational change see: H. A. Gleason in Torrey Bot. Club Bul. **43**: 463-481, 1917; **53**: 7-26, 1926 and Wm. S. Cooper in Ecology **7**: 391-413, 1926. Other discussions are by S. A. Cain in Ecol. Monog. **2**: 475-508, 1932, and by F. E. Clements in Jour. Ecol. **24**: 252-284, 1936.

Carex lasiocarpa around the edge to form an ecological association. This sedge differs from the other plants which one may find in similar situations in that its rhizomes do not maintain a given depth below the surface of the bottom, but grow out into the water. Subsequent interlacing of rhizomes and roots forms a mat buoyed up in the water and capable of growth over any depth of water. Then, provided the ice work and wave work of each year do not wholly obliterate the growth of the season, the mat adds to itself year by year. It soon loses contact with the bottom, if the depression is of sufficient depth. From its lower side detached pieces sink and build up the bottom.

When such a mat has developed, ice seldom does much damage, although it may be able to tear the shore connection out so that pieces of the mat float unattached, at the mercy of the wind. Such a mat is independent of the bottom and can proceed out over the water as far as it can develop vegetatively and is not hindered nor prevented by opposing factors. The development of a mat is one of the specific characteristics of a bog as opposed to a swamp.

Such development tends to push the Nuphar-Nymphaea and Potamogeton associations out into deeper water. If the slope is at all steep, this soon brings about their elimination as they cannot grow beneath nor up through the mat. In a few cases, however, their rhizomes root into the Carex mat and they have been able to keep pace with the advance of the mat. Even here, however, many plants are surrounded and smothered out (Figs. 24 and 25). In shallow depressions these associations may continue to precede the mat to the center of the body of water.

At the shore edge of such a mat, ice frequently grinds vegetation and erodes the shore, thus developing a marginal fosse. Such a fosse may act as a moat, separating the mat from the shore, or various swamp or aquatic plants may develop in the moat unless repeatedly ground out by ice or prevented by the shade of overarching vegetation.

The material of the mat is almost entirely if not exclusively organic material and is the earliest stage of peat.

Such a mat, even when in part tree-covered, is lazily floating and, although not perceptible to the eye, does change in level, floating higher from the bottom in high water years and settling lower in low water years as the following measurements (Table 3) taken in the mat at Mud Lake bog testify (Gates 1940).

A similar fluctuation was recently demonstrated in Cedar Creek bog, Minnesota, by Buell and Buell (1941), where the maximum change of level was 2.3 feet.

Occasionally, particularly as at Smith's bog, conditions have favored an extensive development of the *Carex lasiocarpa* association (Woollett, Dean, & Coburn 1925a and 1925b), but in most places in this region adverse conditions prevent the Carex mat from making more than a fringe of vegetation projecting in advance of the shrub and tree cover. In sheltered bays the mat develops much faster than in exposed places.

TABLE 3. Depth to sand bottom from the surface of the mat at Mud Lake bog.

Year	Depth in feet	Year	Depth in feet
1922	10.5	1932	11.0
1923	10.5	1933	11.7
1924	10.5	1934	11.5
1925	10.5	1935	11.8
1926	10.5	1936	11.25
1927	10.5	1937	11.5
1928	11.5	1938	12.7
1929	12.0	1939	12.3
1930	11.5	1940	12.2
1931	11.0	1941	11.7

In beach pools, such as those along Lake Huron and Lake Michigan, it is problematical whether the pool will develop in the direction of bog, swamp, or marsh aquatic type of vegetation. The kind of plants that ecese determine which type of vegetation will gain mastery. Consequently one finds all types within a short distance of each other, but a fairly large number are developing in the direction of bogs.

Into such a mat come seeds or pieces of certain plants—the invasion of some of which will be followed by ecesis. While in this region herbaceous types belonging to the Iris association may be among the first to enter and form a zone, of greater importance is the invasion of ericads, particularly *Chamaedaphne calyculata, Andromeda glaucophylla* or the cranberry species of Vaccinium. Of these Chamaedaphne is much the commonest in the Douglas Lake region. It produces a low shrub association which gradually replaces the *Carex lasiocarpa* association, but does so on the mat developed by *Carex lasiocarpa*. The tangle of roots holds the partially decayed debris and colloidal material the same as those of *Carex lasiocarpa* already developed. However, the Chamaedaphne mat lacks the ability to proceed out over open water in the easy manner of *Carex lasiocarpa*.

The development of Chamaedaphne makes a shrub association. This association is one of the commonest bog associations in the region. It is also the one least likely to be so severely damaged by a fire that recovery is not prompt.

The Chamaedaphne association is in turn invaded by shrubs which grow taller and shade the Chamaedaphne, finally eliminating it. This association known here as the high bog shrub association has several dominant species, often occurring as consocies. Those most frequently found in this region are the *Salix pedicellaris*, the Nemopanthus, the Salix-Cornus, the Alnus, the *Betula glandulifera* and the Ilex consocies. Each forms thickets which replace the Chamaedaphne on mats which by this time have become grounded.

Following the development of the high bog shrub association one or another tree association is due to

follow. In this region it varies from Larix-Picea-Thuja to Picea-Thuja or Thuja directly. These trees start in any of the previous associations of woody plants, which they eliminate by shading.

With the development of the Thuja association, the final stage of bog vegetational development is reached in this region. Any subsequent development, such as the appearance of the Picea-Abies association is beyond the bog. The same is true where noticeable filling in of bog land has given the maple-beech association a chance to come in, but this of course is beyond the bog. (See succession diagram, Fig. 32.)

DESCRIPTION OF SELECTED BOGS

Before taking up consideration of the associations of bog plants, it may be well to describe briefly the salient features of the principal bogs in the area studied. Where bogs are so numerous and where so many of them fall into well-defined categories, it will be sufficient to describe only a few in detail.

Maple River Drainage Basin

Maple River with its branches is the most extensive drainage system in the central part of the region. Several bogs are associated with this system.

Larks or Round Lake is the headwater of the most prominent branch of West Maple River. Munro Lake (at times of high water), Lancaster, and Douglas Lakes flow into East Maple River, which joins West Maple River in a pond just above the dam, 1.5 miles south of Pellston. A branch of East Maple River comes from the general bog forest southeast of Levering, into which Arnott Lake flows through a small stream soon lost in anastomoses. Formerly an obvious stream flowed from this bog forest northward into the Carp River drainage to Lake Michigan. Now such flow is limited to the time of spring high water. The major drainage is southward into East Maple River and on through Burt and Mullet Lakes to Lake Huron. Throughout much of its course the activities of man have destroyed the typical bog forests along it and in their place one now finds cultivated ground or various mixtures of bog, lowland forest, aspens, and thickets.

ARNOTT LAKE

Arnott Lake is small and mostly shallow with one hole 15 m. deep. Formerly completely surrounded by the Thuja association, at present the land is cultivated to the north. This is the only bog lake, on whose shores phytobezoars have been found (July 19, 1925 at the northeast corner and up to 2 cm. in diameter).

LARKS LAKE OR ROUND LAKE

At the head of West Maple River is a "round" lake about a mile across. Formerly surrounded by a bog forest and with a rather narrow mat, it now has cultivated land to the west and south. To the north and east aquatic vegetation in the water is bordered by a narrow, mostly sandy beach, a prominent, well-formed ice ridge, back of which is a mixture of bog forest, lowland forest and aspen species for a quarter of a mile or more. This forest is one of the three places in which *Carex tuckermani* is found growing in the region.

MUNRO LAKE

One of the largest of the small lakes of the region occupies a low area to the northeast of Vincent Lake. On three sides it is bordered by hills formerly covered with maple-beech forests, now mostly cultivated or abandoned. A ditch now replaces the small stream which formerly drained the lake into Lancaster Lake.

Thirty years ago Munro Lake was 10 to 12 or more feet deep but extensive filling during the recent dry cycle has made it shallow. The former narrow beach in front of a prominent ice ridge has now become a wide flat and the luxuriant growth of *Decodon verticillatus*, extending from the shore out into the water, is now virtually extinct.

A mat is present at the north end of the lake, in which Chamaedaphne has completely overrun the Carex. Chamaedaphne stems lop over into the water, making a sort of floating mat. Back of this are a few bog shrubs and trees.

This bog lake has been the scene of the severest ice work in the region which explains the restricted distribution of the mat. Filling has been from the bottom largely by the work of microorganisms, and has been very rapid in recent years.

LANCASTER LAKE

A small, deep (75 feet) bog lake north of the west part of Douglas Lake is situated in the drainage channel between Munro and Douglas Lakes. The water, when seen in small masses, is brownish in color. Two streams enter at the north corners, the one from Munro Lake, now dry, except for a short while in early spring, and changed to a ditch; the other, with scarcely any water flowing, from tree-covered boggy areas to the northwest. Bessey Creek (or Lancaster Creek as it is called on recent soil maps), flowing out at the south end, drains the lake into Douglas Lake. Wave action has prevented the development of Carex mats except in sheltered coves.

The Potamogeton association in the lake is bordered by the *Scirpus validus* association around much of the lake and this mixes with the Iris association at the shore or abuts directly onto a stony beach in exposed areas of the east side. On the west side, *Equisetum fluviatile* forms a prominent consocies. The mat is best developed at the southern corner of the lake, but it is grounded on a marly bottom on which *Scirpus pauciflorus* is particularly abundant (Fig. 2).

Back from the marginal aquatic vegetation, the original bog vegetation has been completely destroyed. Land to the east is cultivated, that on all other sides is a mixture in varying proportions of aspens and lowland forest, fronted by thickets of Salix, Cornus,

or Alnus, with slight indication of the former bog flora.

A rather well developed ice ridge occurs around much of the lake. Due to its depth and wave and ice action and slight bog mat activity, this lake will be a long time in filling up.

DOUGLAS LAKE

While Douglas Lake itself does not appear to be a bog lake on account of its size, nevertheless some of its bays and coves and former beach pools clearly demonstrate bog potentialities. Particularly is this so of Maple cove, where at the head of the cove a *Carex lasiocarpa* mat has formed and is tending to move out into the water. Great bottom filling, especially in 1916 and 1921 and recent ice and wave work in the shallowing water are distinct impediments to rapid development of this mat. Because of this the higher vegetation keeps encroaching on the mat, as it goes up and down with variations in water levels in different years.

Conditions at Marl bay are suitable to the initiation of bog development. Although the proper species of plants are present, the vigorous ice and wave work break up any newly formed mats. The net effect is little progress. However, bottom filling has gone on quite rapidly, especially since the great building of 1916.

At Hook point, bog conditions are indicated only by shrubs, such as *Myrica gale*, deep in the bay back of the point.

East point is a sandbar which has cut off a series of depressions, only one of which communicates directly with Douglas Lake itself. Bog plants have established themselves in each of the four depressions, although with some admixture of strictly aquatic plants in two of them. The height of the water table in these depressions keeps water at or above the surface. So far this has prevented the invasion of tree associations in three of the four depressions, although plenty of Thuja trees occupy slightly higher ground in the immediate vicinity.

Sedge point is similar to East point in having sandbars which cut off depressions. These sandbars are formed by alongshore waves and windblown currents and are based on a glacial ridge which juts out into Douglas Lake. Of the lakes or ponds formed, the northern and much the largest had water held above Douglas lake level by a Sphagnum ring until this was nearly all burned away in the fire of 1918. The central part had a mixture of bog shrubs and trees, but many of the latter were killed out by

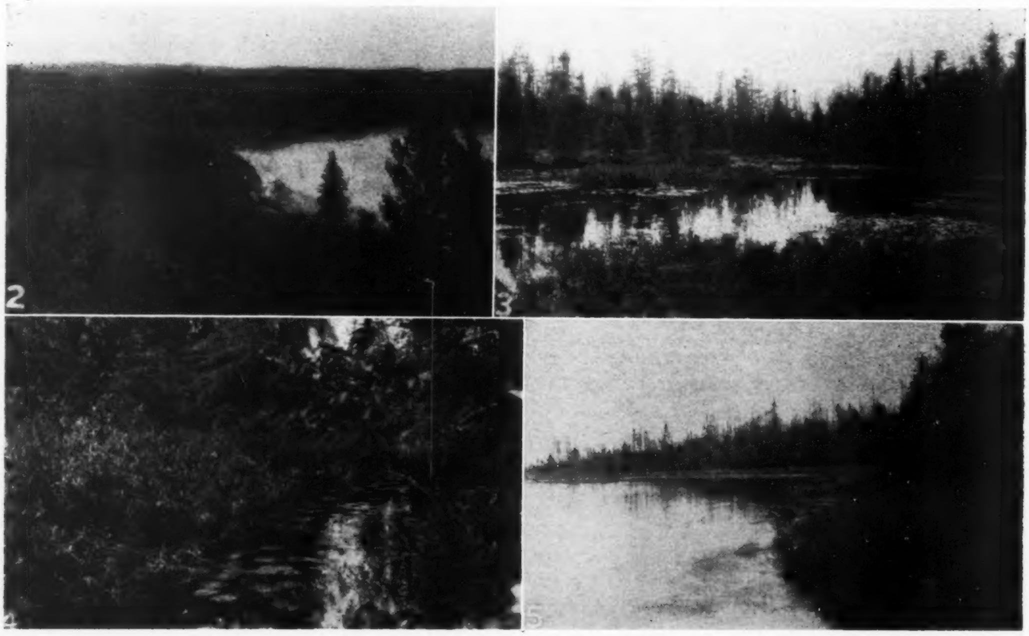


FIG. 2. The southeast end of Lancaster Lake showing bog vegetation encroaching on the lake. July 14, 1923.

FIG. 3. Brown Lake, an expansion of the stream in the Carp Lake system. The stream enters on the left and leaves in the far center. Note semifloating islands of Carex and Chamaedaphne. July 5, 1924.

FIG. 4. The bog stream in the Hebron region somewhat westward from Figure 3. Notice the encroachment of the shrubby vegetation from both sides. July 5, 1924.

FIG. 5. The southeast side of Mud Lake showing the absence of mud at the surface at this time and the quantity of Larix in the background just before the severe attacks of sawfly larvae. July 22, 1916. (Compare with Fig. 6.)

the same fire. The small ponds cut off more recently show admixtures of bog and aquatic plants. No. 4 is now dry. No. 3 is completely changed to land by an influx of sand. No. 2 has a definite *Carex lasiocarpa* mat, now grounded throughout but still maintaining bog physiognomy. A little pond mostly filled with Dulicheum is in its center.

Pond No. 1 of biological station numbering has, within station history, been open to Douglas Lake only in years of very high lake level. This occurred for the last time in 1917. In the earlier years this pond was about 4.5 feet (1.5 m.) deep, but by the growth of aquatic plants together with some sand blown in from the dune ridge to the south is now not more than 2.5 feet (76 cm.) deep and considerably smaller. While some bog species occur around its border, the preponderance of normal aquatics does not indicate progress towards a bog.

Pond No. 0 has been formed since this study was begun. The first indications of a new pond were the appearance of sandbars under water projecting from Sedge point eastward. These bars were worked back and forth, but from 1921 on, yearly accretions were in evidence and the pond was completely cut off in 1939. The vegetation in it is, however, as yet wholly aquatic in nature.

CHEBOYGAN-CECIL BOG

From a little west (5 miles) and south of Cheboygan there extends a long drainage system, nowhere very wide, but with several fingerlike extensions, some of which include bog lakes. In the upper reaches there is no definite stream but the water oozes through the bog forest. A moderately definite stream, at least in high water years, begins in the Mud Lake finger flowing across the Cheboygan-Levering road, where the bog is narrow. After a mile or so it expands into Brown Lake, a small, mat-surrounded bog lake (Fig. 3). The stream (Fig. 4) continues through a tangled bog forest for about 3 miles, then expands into Blanchard Lake (Mud Lake on many maps), a mat-surrounded lake nearly a mile long and wide. Two miles farther on the stream flows into Carp Lake, a body of water about 3 miles long and 0.5 to 1.5 miles across, sufficiently large to prevent a typical bog margin except in sheltered coves. Carp Lake River flows from Carp Lake west and north for about 6 miles and empties into Lake Michigan at the former town of Cecil.

Except for the area immediately adjacent to the various lakes, the whole course consists of bog forests, mostly of Thuja, but often a tangle of Picea, Larix, and *Populus tremuloides*, together with bog shrubs.

The most important fingers of this bog include the one in which Mud Lake occurs and another, which includes a divide in drainage systems, takes in Lancaster, Munro and Douglas Lakes.

MUD LAKE BOG

In the Carp Lake river drainage system an arm projects southeastward into Inverness Township. Near the end of the projection is a lake, about 0.7 km. long and about half as wide, known as Mud Lake (Fig. 5) (Goe, Erickson & Woollett 1924, Welch 1936). The general shape of the basin is that of a broad saucer, with the shallowest depth to sand in the lake 2.8 m. deep and the deepest about 7 m. in the northeastern part of the lake. Early settlers tell of the time when the false bottom was 1.2 to 6 m. below the surface of the water but progressive development of the characteristic organic mud, especially in warm and dry years has brought the mud to within a few centimeters of the surface everywhere, in fact so close that in very dry years the water evaporates to below the surface leaving the mud exposed over wide areas, especially in the eastern and southern parts of the lake. As is usual in these bogs with organic, flocculent, colloidal mud, the lake water is always distinctly alkaline, pH 8 to 9.

Surrounding the lake is a mat of varying thickness and density, formerly floating and quaking throughout. At the present time, however, the mat to the west, north, and south has been firmly grounded and is occupied largely with trees of Picea, Abies (70-90 yrs. old), and Thuja with various mixtures, including even sugar maple, yellow birch, and beech near the margin. The many large trees of Larix, about 100 years of age and 20 meters or more tall, were killed by sawfly larvae between 1916 and 1921 (compare the skyline in Figs. 5, 6 and 7). There has been some lumbering in recent years. This together with class work has greatly reduced the diversity of the ground flora.

Eastward from the lake the mat is more interesting. It extends nearly 1.5 km. beyond the lake. Except close to the lake it is entirely grounded. It has supported a forest of *Picea mariana* and *Thuja occidentalis*, but now over considerable areas in its central and eastern part, following a series of fires, the vegetation is largely dominated by Chamaedaphne, completely so where fires have been most severe. The most recent fire in this area occurred in 1916. Closer to the lake are what appear to be ridges covered with trees of *Picea mariana*. The ridges are sometimes actual depressions, the ridge appearance being due to Chamaedaphne being taller around the bases of the spruce trees. Active layering is responsible for the rapid spread of Picea, but several seedlings are also present. Open water formerly existing back of the row of trees along the lake has now been completely covered up, due to the development of Sphagnums accompanying sedges and the free invasion of members of the Chamaedaphne association. Waterlilies which grew in this area were transferred bodily to sheltered places in Douglas Lake. Their developmental characteristics there demonstrated that the smaller plants in the bog are merely ecological manifestations rather than separate species.

The mat about 46 m. back from the lake is about 76 cm. thick and in the earlier studies seemed to be grounded with a distance to bottom at 10.5 feet (3.15 m.). For years this condition remained, as

tested each year with a Davis peatborer. However, in the high waters of 1928 the mat broke away and became floating. Peat samples were no longer obtainable from the mat nor even for quite a distance below it. Attention was called to this fluctuation in a recent article (Gates 1940) and earlier in this paper. It is interesting to watch a tree-covered mat rise and fall with the years.

Beneath the peat in this bog is a layer of blue clay 10-15 cm. or more in thickness, in which are many shells. The following species have been recognized by Dr. Frank C. Baker:

Fossaria obrussa decampi (Streng)
Gyraulus deflectus obliquus (DeKay)
Amnicola limosa porata Say
Physa integra Hald. Var.
Helisoma antrosum striatum (F. C. Baker)
Helisoma campanulatum (Say)
Gyraulus altissimus (F. C. Baker)
Valvata tricarinata (Say)
Valvata tricarinata simplex Gould
Valvata lewisi Currier
Pisidium species indet.

They are all species characteristic of the last stages of the Late Wisconsin section of the Glacial Period.

The lake is sufficiently large to permit wave action which has been effective in preventing more rapid closing in on the lake. However, in protected corners, the mat has pushed out 30 to 130 cm. during the present study and in the inlet of a small streamlet, now hardly ever running, the mat has built itself out over 46 m. since 1916 (Figs. 6 and 7). With the organic mud so close to the surface, patches of mat, but more frequently clumps of Chamaedaphne, are broken off from the mat by ice and are moved along shore by wind and ice, often reaching the eastern edge of the lake where they form accretions to the mat. The history of several such clumps has been followed.

However, ice work and wave conditions prevent the development or have broken up the *Carex lasiocarpa* edge. In such places the progress out into the water is made by Chamaedaphne, but with the soupy gelatinous condition of the organic mud this is very slow. The Chamaedaphne bushes lean out and fall under the water and mud at the edge as new shoots grow

FIG. 6. View of the southeast corner of Mud Lake, looking across exposed mud to the tree vegetation in the background. Note the clumps of *Carex lasiocarpa* and other vegetation floating in the mud, muskrat runways and, at the far edge of the lake, *Carex lasiocarpa* mat (light color) followed by a narrow zone of Chamaedaphne (completely overrunning at the right), the high bog shrub, and the Picea association in which a considerably quantity of Thuja is invading. Compare with Figure 5 to contrast the loss of Larix which formerly dominated the bog woods here. (Photograph by C. H. Blair. July, 1939.)

above. Ultimately it is to be expected that as the organic mud gains density greater progress out over the water will be made and the lake will slowly but surely be obliterated.

BLANCHARD BOG

Blanchard Lake, known as Mud Lake on county maps, is an expansion in the Cheboygan-Cecil bog. The main body of the lake is relatively shallow with *Scirpus acutus* and *S. validus* mostly around the edges but also to a limited extent in the center. A rather broad mat is present on either side extending up into the woods at each end of the lake (Fig. 8). *Carex lasiocarpa* is the principal species, although on this mat there were more species than one usually finds on a Carex mat. The mat was loosely grounded for the most part with many areas quaking. Over the deepest part of the basin discovered was a firmly grounded mat which supported a dense thicket of bog shrubs and a single tall rapidly growing *Pinus strobus* tree about 45 years old (Fig. 9).

Bog shrubs lined the mat landward, giving place to the Larix association or a Larix-Picea-Thuja mixture, except where a dense stand of aspens indicated previous fire.

In 1933, beavers built a dam across Mud Creek below the lake. The subsequent rise in water level loosened great masses of the mat from the bottom, restoring it to quaking. However, the large outstanding pine was too firmly rooted to ride up on the water and it drowned. The same fate was in store for the many trees of Larix, most of which were about 130 years of age.

Subsequent lowering of the lake with the extinction of the dam has left a general mixture of various bog elements but without the former most interesting features.

VINCENT LAKE

This small bog lake is located in a kettle hole surrounded by maple-beech covered hills. Streams neither enter nor leave this lake. Formerly the water of this lake was decidedly acid (pH 4.5) but in recent years, following lumbering in the vicinity, dry

FIG. 7. A view over the southeast corner of Mud Lake showing the great expanse of organic mud filled in since 1916. The man is standing at the 1921 edge of the open lake. The species present on this mat are given in the text under the discussion of Mud Lake. July 21, 1937.

FIG. 8. View at the east end of the Blanchard Lake bog. In the foreground the extensive mat of *Carex lasiocarpa* with many invasions of *Chamaedaphne calyculata*; in the background, the high bog shrub association is followed by the Larix association. These trees are about 125 years of age. All were drowned a few years later. August 5, 1929.

FIG. 9. The mat in the deepest part of Blanchard Lake basin, including a "vegetation island" with several bog trees and in the center a *Pinus strobus* estimated to be about 50 years of age. (Photograph by T. P. Haines, August, 1932.) (A few years later inundated as the result of persistent flooding following construction of a beaver dam and all of these trees were killed.)

FIG. 10. The east shore of Vincent Lake. *Eriocaulon articulatum* is abundant on the sandy, mucky marl. Bog vegetation surrounds the lake. August 9, 1919.

cycles and fires nearby, the pH in most years now is near the neutral figure.

The lake vegetation includes various Potamogetons, Isoetes (now extinct) and *Eriocaulon articulatum*. Wave and ice action have kept the mat from developing out from the shore, but just back from the shore is a zone of bog shrubs and trees including Chamaedaphne, Alnus, Picea, and Thuja.

On the east side of the lake a flat (Fig. 10) used to be just below water level and covered with *Eriocaulon articulatum*, until low water years when it was exposed and quickly vegetated with seedlings of *Betula papyrifera*. High water in their third year, however, drowned them out. The Eriocaulon, formerly so abundant, has not come back in any great quantity however.

GATES BOG

Southeast of Vincent Lake, in a broad depression in the upland is a Chamaedaphne bog. Mere traces of the former body of water are indicated by a little standing water in the west part during highwater years. In this part *Scirpus atrocinctus* and members of the Iris association are in evidence. Otherwise the vegetation of this bog is Chamaedaphne with several species of Sphagnum. Fires have repeatedly burned over parts of the bog, but in the absence of fires in recent years, the aspens are appearing in small numbers in the eastern third of the bog. Land formerly vegetated with the maple-beech forest entirely surrounds this bog.

This bog is of special interest in having been the habitat of a larger number of species of Sphagnum than any other in the region so far as known. The following species were collected in late July, 1928 by E. H. Moss.

Sphagnum capillaceum	frequent
" *capillaceum tenellum*	frequent
" *compactum*	locally abundant
" *cuspidatum*	abundant (pools)
" *fuscum*	frequent
" *imbricatum affine*	local
" *magellanicum*	abundant
" *papillosum*	local
" *recurvum*	abundant
" *subbicolor*	local (in shade)
" *subsecundum*	frequent

LINNÉ BOG

Linné bog is a small peat bog, 90 by 70 meters in extent, in a shallow depression in a glacial moraine southwest of Wolf's bog. For the most part the bog is in the Chamaedaphne stage of development. Patches of *Carex rostrata* have (1921) entirely replaced the irregular winding pools of water formerly present in the center of the mat and Nemopanthus has freely invaded the periphery.

Prior to lumbering in 1911, there was a small pond about 60 cm. deep, at the edges of which ducks nested. Now the bog is without apparent inlet or outlet and in most seasons is dry. The vegetation on all sides was maple-beech forest, now under sporadic cultivation. Fire burned through the bog in 1919. (Confer Dean & Coburn 1927).

WOLF'S BOG

A shallow depression, approximately a square mile in extent, in the northern part of sections 13 and 14 in Munro township of Cheboygan County is vegetated largely with bog associations. It has been the source of cedar posts and lumber for several years. The former small lake in the northern part was transformed into a sawmill pond but with the abandonment of the mill, has now filled in completely. Sluggish streams flowed into the lakelet from the northeast and south but now water is seldom present during the summer.

The present-day vegetation consists of Thuja areas in much of the eastern half with irregular mixtures of bog trees and shrubs and aspens elsewhere. Part of the edge of this bog has been burned over thoroughly and is now a pasture.

Seventy years ago this bog was completely dominated by *Thuja occidentalis*. Here were the largest Thujas ever found in the immediate Douglas Lake region. The trees were from 60 to 100 cm. in diameter. The age of one of the largest was counted and estimated to have been about 400 years. Even now the second growth Thujas are large compared with Thuja of similar age growing in other parts of the region.

The organic accumulation in Wolf's bog is mostly about 35 cm. and does not exceed 90 cm. anywhere. In the deepest deposit found the hydrogen ion concentration expressed as pH varied from 7.4 from the surface to 10 cm. deep, 7 at 20 cm., 6.94 at 30 cm., 6.90 at 40 cm. and from there on down it remained at pH 6.86.

During two summers' work (1936-37) in this bog, Ruth Dutro and Edith Cohoe found 270 species of plants, representing 54 families of flowering plants, 3 of ferns and 18 of Bryophytes (Dutro & Cohoe 1938).

However, with the general drying of the region and the number of deciduous forest elements in this bog, especially seedlings and saplings of beech and sugar maple, even in the subclimax Thuja, the successional tendency towards the maple-beech forest, the climax of the region, seems apparent.

BRYANT'S BOG

A small kettle hole, nearly circular bog 107 by 115 m., near Bryant's resort is known as Bryant's bog. Notwithstanding its small size, it is one of the deepest in the region. Smoothing the profile of the measured depths indicates that the bottom is approximately 22 m. below the surface of the lake. Although separated from Douglas Lake by but a comparatively few meters of sandy, gravelly ridge, the Sphagnum ring maintains the pond (Silver Lake) in the bog at an elevation of approximately 0.9 m. above Douglas Lake.

A small, somewhat crescent shaped pond lies in the center of the mat. (Cf. Welch 1936.) It has noticeably decreased in size within the course of this study, as is shown on the accompanying map (Fig. 11).

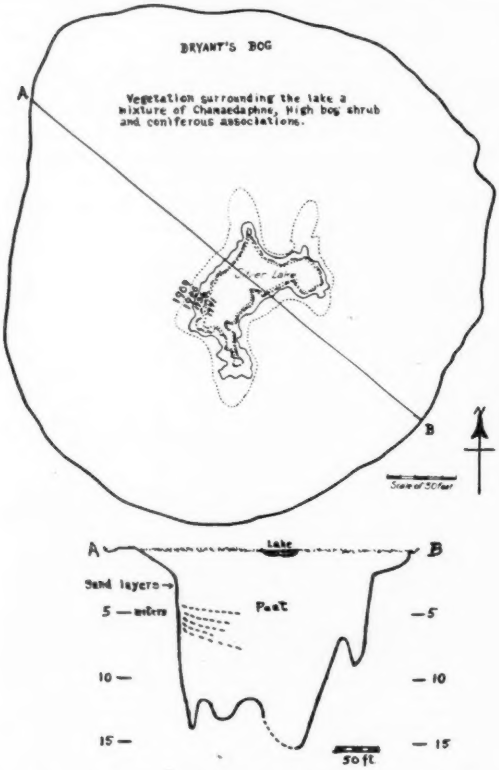


FIG. 11. Map of Bryant's bog showing the shrinking outline of Silver Lake for the years indicated. Below is a profile of the bottom along the line A-B, constructed from data obtained by Helen Coburn, Doris Dean, and Gertrude M. Grant in 1927. Note the steep sides of the depression and particularly the thin (2 to 9 cm.) layers of sand projecting from the west side out into the peat.

When first known the false bottom was about 5.2 to 5.8 m. below the surface of the water and no plants were observed growing on it. A 6-pound sounding lead would sink to about 9 m. but steel rods subsequently disclosed the much greater depth to sand. The false bottom was 4.6 m. below the surface in 1912. In the very hot, dry summer of 1916, the great activity of microscopic organisms resulted in the upbuilding of this false bottom to within 3.4 m. of the surface and in 1917 there appeared a thin sterile growth of what later was found to be *Scirpus subterminalis*. From that time on oxygen content rose and green algae appeared. In 1918 the false bottom was 2.3 m. deep and sounding lead went to 5.5 m. In the next hot dry year (1921) phenomenal activity of microorganisms again caused a great rise in the false bottom in this and other bog lakes, coves, and bays. In Silver Lake the rise of the false bottom was to 60 cm. below the surface and Potamogetons, *Utricularia intermedia*, and waterlilies appeared on it. Since that time rise has been more gradual and the stage depends upon the dryness of the summer, closer to the surface in dry years (even to a few centimeters) and deeper in wet years.

Extensive steel rod plungings have made possible the preparation of a contour map of the bottom of this bog. (Coburn, Dean, & Grant 1932, p. 59.) A shelf dropping off to a deep hole is a prominent feature shown in this map. On the west side of the bog, at least five sandy layers of 2.5-5 cm. in thickness, beginning about 4.6 m. down, separate the organic deposits above the actual sandy bottom of the bog. The absence of equipment to sample each small interval through such sand layers makes it impossible to say much regarding the past history, but pollen studies of the upper peat layer, made by Potzger in 1931, emphasize the great preponderance of deciduous tree pollen over coniferous pollen in the upper 8 feet (2.5 m.), a relationship which does not exist at lower levels.

Methane is formed in moderate quantities under the bog mat. It ignites readily and occasionally is tapped with explosive cores. The fosse around this bog, although discontinuous and now poor in most places, still is one of the better fosses seen in the Douglas Lake region.

Human activities are now common in this bog. They have broken up the *Carex lasiocarpa* mat and stirred up the lake. Collecting in the study of this most interesting bog has reduced the flora from more than 80 species to less than 30 species of higher plants and ferns. It still remains, however, as one of the most beautiful little bogs in the region.

When first known a *Carex lasiocarpa* mat surrounded the lake and bid fair to cover the lake completely. It did proceed rapidly in filling the deep bays of the earlier outline, as shown in the map (Fig. 11), but after human activities destroyed the narrow zone of *Carex lasiocarpa*, closing in on the lake has become a slow process. It was too deep for Chamaedaphne to make any headway out into or over the water (Figs. 12 and 14). Now, however, with the filling up of the false bottom to a density sufficient to hold up heavier plants, a gradual but slow reduction of the surface of the lake is going on.

In earlier days this bog must have been a Thuja or a Thuja-Picea bog, as shown by pollen deposits and by logs buried in the peat. Fires at a date considerably earlier than the founding of the Biological Station swept over the bog. A Chamaedaphne stage evidently occupied all of the mat back of the edge of the *Carex lasiocarpa* association and succession had gone forward briskly into it at the time the bog was first observed. At that time a fringe of Larix and *Picea mariana* trees nearly surrounded the lake; the west and south halves were largely vegetated with the Nemopanthus consocies of the high bog shrub association, into which various trees, in-

cluding *Larix laricina, Picea mariana, Pinus strobus, Populus tremuloides,* and *Betula papyrifera* occurred irregularly distributed. The remaining northeast third was a typical example of the Chamaedaphne association. By 1917, seedlings of *Nemopanthus mucronata* began to make their appearance in this Chamaedaphne; in 1921, they were just below the level of the Chamaedaphne. Topping the Chamaedaphne began in 1922 and by 1925 all of the northern and eastern parts of the periphery of Bryant's bog had passed into the Nemopanthus consocies stage. Into this, trees have been slow to invade.

GLEASON'S BOG

In another depression a short distance east of Bryant's bog occurs a figure-8 shaped bog. As this bog is close to the level of Douglas Lake, although separated from it by a ridge vegetated with maple-beech, it always has some standing water, except during exceptionally dry summers when Douglas Lake becomes very low. Up to 20 years ago a small open pond was present near the north end. This is now completely obliterated by the growth of Chamaedaphne, the dominant plant throughout the bog.

When first studied this bog had an incomplete fringe of high bog shrub association and a still more broken fringe of Larix and Picea, especially on the west side. Fires set to encourage blueberries in the vicinity have completely destroyed all evidence of former coniferous trees several years ago. Available seed trees are only about a kilometer away, but no seedlings have appeared. The high bog shrub association, represented especially by *Aronia* spp. and Nemopanthus is now rapidly occupying the ecotone between the bog and the aspens surrounding. The entire center of the bog is vegetated with *Chamaedaphne calyculata* with an abundant growth of species

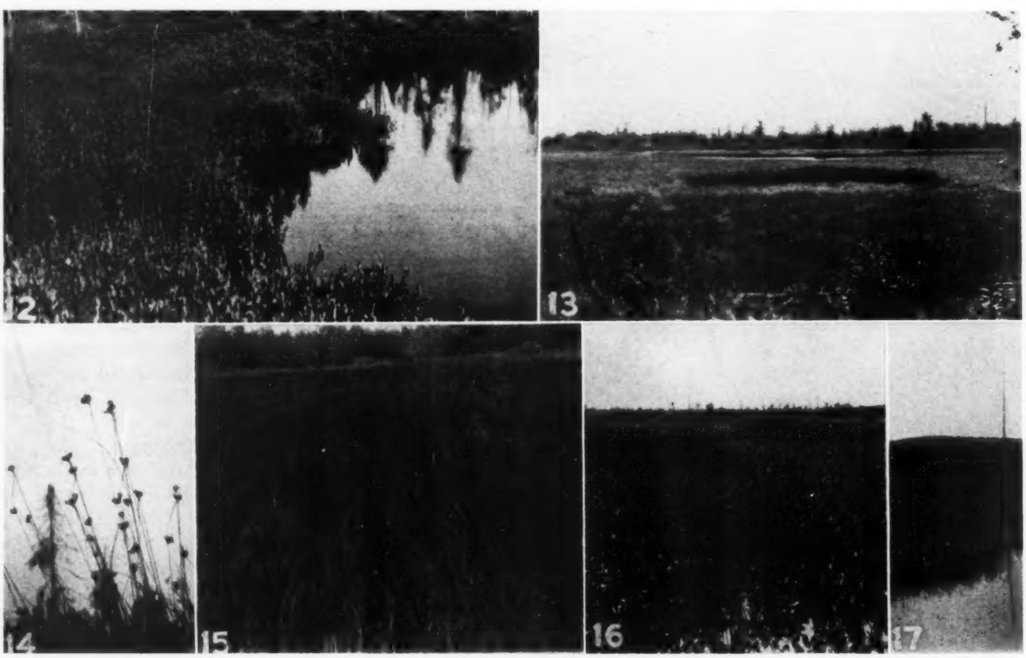


FIG. 12. The edge of Silver Lake in Bryant's bog showing the Chamaedaphne association attempting to grow out in the water following the breaking up of the original *Carex lasiocarpa* mat, of which a small piece still remains in the center. July 15, 1916.

FIG. 13. Smith's bog from the northwest. In the years following the lake has contracted to about a sixth of the size shown here. Chamaedaphne has spread around the edges of the lake and at the edges, the high bog shrub association represented by *Salix pedicellaris* has fairly well covered the area to the left of the lake. In the immediate foreground fire has seriously damaged the *Carex lasiocarpa* mat. August 1, 1915.

FIG. 14. View of *Eriophorum virginicum* taken diagonally upwards from the surface of the mat. Eriophorum quickly fills disturbed areas in Chamaedaphne for a few years. In the foreground the plants of Chamaedaphne and in the background is a tree of *Picea mariana* showing the witches broom development after infestation with *Arceuthobium pusillum.* Such trees die within a few years. (Photograph by Christine Radebach, July, 1932.)

FIG. 15. A general view of a characteristic *Carex lasiocarpa* association at Smith's bog. July 19, 1929.

FIG. 16. A view near the mouth of Maple River showing mats of *Menyanthes trifolia, Typha latifolia* and *Phragmites communis* with the lowland forest in the distance. August 7, 1920.

FIG. 17. A view along Indian River showing *Thuja occidentalis* invading the compact Typha mat. July 21, 1929.

of Sphagnum, a few plants of *Menyanthes trifoliata* and little else.

Two other kettle holes to the east are lacking in any evidence of having been occupied by bog plants, since fires have burned out the soil. Gleason's bog, however, with a bottom below the water table level of Douglas Lake, will remain a bog until the kettle hole becomes filled up or the level of Douglas Lake is distinctly lowered.

NIGGER CREEK DRAINAGE SYSTEM

Into Mullet Lake a little north of Topinabee flows a small stream, known as Nigger Creek. The stream itself is sluggish, although in some places deep. In the water the Potamogeton association is well developed, likewise the Nuphar-Nymphaea, including here beds of *Rorippa palustris,* whose easily detachable leaves float down stream. The Iris association borders and is followed by bog shrubs. About 3 km. upstream from Mullet Lake, the stream is very small and is bordered by bog trees.

The upper area of this stream is known as Riggsville bog, a compact area of bog trees mixed with postpyric vegetation. A finger of this area includes Smith's bog, from whose lake a tiny stream used to flow in the vegetation.

SMITH'S BOG

An expansion of a finger from the Riggsville bog, containing a small pond or lakelet presents striking characteristics and is known to us as Smith's bog (Fig. 13). When the author first saw this bog in 1911 it had a lake occupying about two-fifths of the depression, and surrounded by an excellent *Carex lasiocarpa* mat (Fig. 15) at a distinctly higher level than at present. Landward the Chamaedaphne-Sphagnum did much to hold the water level up. Next came high bog shrubs and then bog trees, as *Picea mariana* and *Thuja occidentalis.* East of the bog is pine land; west, a maple-beech forest with a wide transition zone; southwest, a cultivated field; and south, a basin occupied in part by trees of maple-beech affinity, in part lowland forest, and in part bog. To the north the tree-covered part is continuous with Riggsville bog to the northeast.

Later Professor Frank Smith discovered that this bog contained all the species of freshwater sponges then known to inhabit the region and it became known as Smith's bog.

Lumbering and fires in the vicinity destroyed the surrounding vegetation and invasion of aspen followed. Fire in 1914 and a very severe fire in 1916, burning out onto the mat, destroyed the Sphagnum fringe besides burning up some of the peat at the edges. Likewise all of the Picea and Thuja present were destroyed by fire and neither of these have since reappeared. Following this fire the floating mat became grounded. The last part to ground was that west of the center of the little lake. Sphagnum is now reappearing in spots around the edge, but it is questionable whether a new lake or a larger lake will redevelop. Meanwhile, the Calamagrostis meadow which came in on a part of the burned Carex mat near the shore is spreading at the rate of about 10 to 30 cm. a year.

A few seedlings of *Chamaedaphne calyculata* appeared about 1918 on the floating mat and in 1920 partly rotting, shrub-covered logs were worked out from the shore to the east border of the lake. From these two sources Chamaedaphne has formed a border to the lake to the east and north. With the firm grounding of the mat succession became rapid as shown by the celerity with which *Salix pedicellaris* extended the boundaries of the high bog shrub association, especially from 1932 on. This succession is particularly in evidence north of the lake, where *Salix pedicellaris* is increasing noticeably. It reached the lake in 1938. Closing in on all sides is evident also, but on a smaller scale than at the north.

Closing in at the south has all but obliterated the expansions in the little stream that flowed slowly into the lowland forest, where it seeped into the soil, and presumably reappeared as part of Fontinalis Run. Where 10 years ago standing water was always present in the lowland forest, now there is none except in early spring.

Neither blue clay nor marl has been found in this basin, only an accumulation of Carex peat and organic mud. In earlier years the water in the lake was always distinctly acid (pH 4) but since the organic mud reached the surface in recent dry years the waters of the lake test pH 7, but the Carex mat still remains from pH 5 to 6.

In the disturbed parts of the southern third *Typha latifolia* was plentiful, but following abandonment of the adjacent farm, the crest of Typha domination has passed and year by year it is dwindling away. *Carex rostrata* likewise no longer makes the showing that it formerly did.

As this bog has been the location of most of the intensive studies of the *Carex lasiocarpa* association, further details regarding Smith's bog should be sought under the discussion of the *Carex lasiocarpa* association itself. (Woollett, Dean, & Coburn 1925a, 1925b.)

REESE'S BOG

Across the head or north end of Burt Lake is a bog, about 3 km. across and from 0.8 to 1.5 km. or more in width, made by the encroachment of vegetation upon Burt Lake. This bog reached maturity long ago. It had re-established the Thuja association when this study began. Carp Creek, the underground drainage from Douglas Lake, flows through this bog and seepage streamlets are also present.

During the years that this bog has been under observation, conspicuous building up has been taking place. Former wet areas are now dry, standing water is seldom seen, and the former fosse at the north end has been completely filled by the building up of the vegetation together with sand blown in from the hogback ridge immediately north.

This large bog has contained the largest number of species of plants of any of the bogs, but with the increasing density of the trees, the closing in of trails and open places where trees have been logged, the flora is diminishing perceptibly. Successions from fires and flooding, concurrent with beaver activity, maintain diversity.

This area will probably be the finest example ot the climax association of bogs available to the next generation of students.

HOGBACK BOG

A small (64 by 107 meters) peat bog, 0.15 km. west of Carp Creek, and south of the hogback road, has been known as the Hogback bog. Although 5.3 meters above the stream in the gorge so close to it, there appears to be no drainage into Carp Creek because of an impervious clay bottom. The small amount of standing water in the bog comes from rainfall and from seepage from the adjacent ridge. In 1925, this water was decidedly acid, pH 3.3.

The entire mat is grounded and the maximum depth to sand is but 0.6 meter. Removal of Sphagnum, including the accompanying Chamaedaphne for commercial purposes, as well as aggressive insect work on Chamaedaphne, maintained open water much longer than would otherwise have been the case, but ultimately Chamaedaphne, followed by the high bog shrub, dominated by Nemopanthus is expected to occupy the center.

Trees of *Larix laricina, Picea canadensis, Pinus strobus* and *Pinus resinosa,* already occupying the periphery, will be expected to spread out over the bog in the absence of fire, or Picea and Thuja may occupy the lower and wetter portion with pines at the periphery. (Confer Sigler & Woollett 1926.)

Southwest is a smaller bog. It is even drier than the Hogback bog. The center is occupied by Chamaedaphne and Sphagnum. *Aronia arbutifolia* and *Nemopanthus mucronata* occupy the edge. Scattered trees of *Populus tremuloides, Picea canadensis* and species of Pinus are present in and near this bog.

NICHOLS, LIVINGSTON, AND VESTAL BOGS

Within 1.5 km. east of the north end of Burt Lake are three bogs of rather simple structure. A narrow bog with lakes at each end lies a few meters south of the road. All of the area has been subjected to lumbering and other human interference, if not actual burning. A small sawmill was located at the east end some years ago. At the present time the lake in Nichols bog is largely surrounded with hummocky, grass and sedge covered ground, only part of which is in any way typical of bog lakes. This area is continually grazed.

West from the lake, Nichols bog narrows considerably and becomes Chamaedaphne covered with the center an admixture of Picea, Larix and high bog shrub. On the south the bog abuts against maple-beech forest, while on the north a zone of aspen conceals the boggy part from the road. In this central part occur a few small and one large open area, thoroughly dominated by *Chamaedaphne calyculata.* Although now entirely covered with *Chamaedaphne calyculata* and surrounded by a fringe of Picea, Larix, and an occasional *Pinus strobus,* the open area was probably at one time a small lake intermediate in size between the lakes at either end of the bog.

LIVINGSTON BOG

In the western part of this boggy area is a narrowly oval, shallow lake, in a deep basin completely surrounded by Chamaedaphne. At the edge the bushes of Chamaedaphne lop over into the water and no trace of a *Carex lasiocarpa* association is present. The lake itself is 70 by 28 meters, with the false bottom but little below the surface. Sandy bottom is more than 9 m. below the level of the lake.

Just east of the lake, the mat is 1 to 2 m. thick, below which methane gas is abundant. A peat borer can get samples to a depth of about 8 m., but a steel rod can be forced down to a depth of 14 meters. The last 2 to 2.5 m. is through a dense layer of clayey sand, quite hard near the bottom.

The Chamaedaphne area is surrounded with high bog shrub or layering clumps of *Picea mariana* with an occasional *Larix laricina* and *Pinus strobus* or a mixture of both in which the large fern, *Onoclea strutiopteris* is often abundant. These in turn are followed by maple-beech on the south and aspen on the north.

VESTAL'S BOG

About 0.8 km. south of Livingston's bog and entirely surrounded by maple-beech forest there was a shallow bent-eight shaped lake, which now has become filled up. The last vestiges occupied by the lake are now vegetated by plants of Eriophorum and *Carex rostrata.* Even these are being closed in by the Chamaedaphne which occupies almost the whole of the basin. At the edges a zone of high bog shrub, consisting largely of *Ilex verticillata,* and Nemopanthus occurs. The deepest depth to sand measured was but 2 meters. Open water was last observed in 1927.

Encroachment by the maple-beech forest is indicated, but is taking place slowly.

THE INLAND WATER ROUTE BASIN

This drainage system of several rivers and lakes formed an important shortcut in travel from Little Traverse Bay to Cheboygan in days gone by. Although belonging to bog classification, most of the lakes, being fairly large, have had their shores wave and ice worked to the point of disintegrating any mat that may ever have been present. Dredging the streams and boarding the banks of some have destroyed former typical bog vegetation and have prevented its redevelopment. Nevertheless plenty of evidence is available to indicate the proper nature of these streams and lakes.

Beginning just north of Petoskey a very short distance (0.6 km.) from Little Traverse Bay of Lake Michigan flows a little stream northeastward. Its widest part, which is 4 m. deep, is known as Mud Lake. From this stream to the bay was the early Indian portage of less than 0.6 km. Less than 1.5 km. to the northeast the stream expands into Round Lake, a bog forest surrounded lake a little over 1.5 km. across. The stream, continuing eastward, is now carried under the railroad in a conduit and empties into Crooked Lake. This lake is well named. It is about 6.5 km. long and up to 2.8 km. wide and in the center 8 m. deep. Where now natural, its shore is vegetated with aquatic plants in contrast to bog species, except near the outlet, where there is a considerable development of bog mat. On the south the principal drainage accretions are Minnehaha Creek and the stream which drains Pickerel Lake, the latter a body of water about 4 km. long and 1.5 km. wide, up to 20.3 m. deep, whose shore shows great ice activity.

Crooked Lake drains into Crooked River, a maintained waterway, 9 km. long draining into Burt Lake. Along Crooked River is a bog mat, now largely grounded and alternating occasionally with sandy shores and lowland forest clear to the stream. The bog forest, now of course quite mixed in composition, is rather extensive along much of this stream but gives place to marshes near the outlet. A little down stream from Alanson, a wide expanse through which the channel has been dredged is known as Hay Lake. In it is a mixture of typical aquatic and bog mat plants.

Burt Lake is one of the two larger lakes wholly within Cheboygan County. It is about 17 km. long and 4 to 8 km. wide and 19.5 m. at the deepest. Severe wave and ice action have maintained a sandy or rocky beach, except in the protected bays into which Maple River and Crooked River flow. In these two bays the vegetation partakes more of the bog character than anywhere else along the shore (Figs. 16 and 20). Reese's bog forms a "cap" at the north end of Burt Lake.

From the southeastern corner of Burt Lake flows Indian River, a dredged channel about 6.5 km. long, emptying into Mullet Lake. The upper part of this river is hemmed in with docks, but beyond the inlet of Little Sturgeon River a grounded bog mat is in evidence, which towards Mullet Lake becomes a floating mat. An originally extensive bog forest of Thuja along the stream is plentifully evidenced, but ravages of man and fire have been severe. The present mat (Fig. 17) is vegetated with a very heterogenous mixture of bog and aquatic plants, dead trunks of trees, in and around which are boat lanes, together with irregularly distributed floating masses of mat. Toward the outlet open water is more in evidence and the mats are composed of *Menyanthes trifoliata* grading into the Scirpus of the protected open lake.

Mullet Lake, the other of the two large lakes of this system is about 16 km. long and 2.4 to 6.5 km. wide and 44 m. deep at the deepest. As an open body of water its shores show much evidence of ice and wave work and comparatively little of any typical bog developments. Minor streams, such as Nigger Creek, and the larger Pigeon River flow into it. It, itself, empties into the Cheboygan River, which in the course of its 10 km. receives Black River and empties into Lake Huron at Cheboygan. Evidences of their essential bog nature are now largely destroyed.

NORTHEAST QUARTER HEBRON TOWNSHIP BOGS

In the northeast quarter of Hebron Township are a few bogs which have been given a modicum of attention during the years.

MALONE (MALONY) LAKE

A small, moderately deep roundish lake, about half a kilometer across is surrounded by typical bog vegetation (Fig. 18). Only isolated remnants of a former *Carex lasiocarpa* mat remain. The mat is nearly completely overrun with Chamaedaphne, whose progress toward dominance has been materially assisted by repeated fires. *Eriocaulon articulatum* growing in this mat at the water edge a few meters above the real bottom is one of the features of this bog. Irregular patches of the high bog shrub association are scattered here and there on the landward side of the Chamaedaphne. Partly mixed in with them and, forming a ring at the periphery of the bog, is the Aspen association, in which are a few conifers. The water of the lake is alkaline (pH 8).

Across the road from Malone Lake is a small Chamaedaphne area, carried on many maps as a lake. Although it may have been a lake many years ago, it is now and has for many years been a Chamaedaphne area in a low spot in the aspens.

PENNY LAKE

A little over 1.5 km. southwest of Malone Lake is another small lake, about twice as long as broad, known as Penny Lake. This lake is at the extreme eastern edge of an extensive bog, at least 4 km. long and in part over 1.5 km. wide. This bog has been so many times and so thoroughly burned over that the former bog trees are virtually gone and even much of the peat has been burned up. In some places this peat was 1.5 m. or more deep. The severe fire of 1927, which burned up so many of the trees in many places, burned this peat down below the average water table level. An abundant growth of *Agrostis scabra* covered this extensive area, except where *Scirpus atrocinctus* developed prolifically in lower spots a few years later and became the fuel of an extensive hot fire in 1931 and again in 1939.

Close to the lake the mat is covered with Chamaedaphne with a fringe, now partly burned up, of *Picea mariana* with a few *Larix laricina*. In the water *Eriocaulon articulatum* and *Sparganium minimum* form well-defined patches on the organic mud.

The oldest stem of *Chamaedaphne calyculata* yet located in this region was found at the northeast corner of the lake. It was 11 years old.

NELSON LAKE

A small, very shallow lake lies across a road about 5 km. east of the end of Carp Lake. In dry years no water is visible. In the lake the vegetation is quite largely Scirpus and marsh with sedges and grasses. Patchy remnants of the high bog shrub association occur here and there at the edge where severe fires have not quite devoured the edge.

FINSTER MARSH

A small, shallow depression southeast of Nelson Lake is known as Finster Marsh. Water is visible except in the driest years. The typical bog associations have been disrupted by fires, leaving the present vegetation a heterogeneous mixture of bog and wet ground species. The area is of interest because of the presence of quantities of *Alisma subcordatum*.

BLACK LAKE

At the extreme east central part of Cheboygan County and extending over into Presque Isle County is another large lake, 9 km. N-S and W-E. Its open waters with their wave and ice work have kept its shores sandy or rocky except in protected bays where a mixture of aquatic and bog mat plants is present.

Upper Black River drains an extensive area of the southeastern part of Cheboygan County into Black Lake and Black River drains it into the Cheboygan River.

SOUTHEAST CHEBOYGAN COUNTY

The southeastern part of Cheboygan County has many small lakes, many of which have not been studied in the course of this work, but such as have been studied are similar to those in the northern parts of the county.

WEST LAKE AND EAST LAKE

Along U. S. Highway 31 a short distance north of the east end of Carp Lake is a pair of lakes, which are designated as East Lake and West Lake, one on either side of the highway. Both are shallow, approximately circular, in depressions in pineland and about 0.3 km. in diameter, not sufficiently large for any important wave or ice action.

In West Lake the shallow open water of the center is surrounded by a zone of *Scirpus acutus* running into a *Carex lasiocarpa* mat which has irregular patches of Mariscus, etc., and giving place entirely to the Chamaedaphne association which forms the outer bog association. Here and there invasion of high bog shrub species is noticeable and even a few small trees may be seen. On the whole, however, the peripheral vegetation has been so disturbed by various fires, that the complete series of bog associations has no chance to develop.

The main part of the mat around East Lake, on the other side of the highway, exhibits less evidence of disturbance, although the periphery has been subjected to fires often enough to have the surrounding vegetation aspen instead of pine. The shallow open water of the center is surrounded by an excellent *Carex lasiocarpa* mat, except as a few patches of *Typha latifolia, Scirpus acutus* and *Nymphaea odorata* appeared in the recent low water years, when organic mud developed greatly and appeared close to the surface. Scattered through the lake are plants of *Scirpus acutus*. The *Carex lasiocarpa* mat is particularly well developed, about 10 meters or more wide, perfect except as a few plants of the wet meadow grass, *Calamagrostis canadensis* have invaded during the recent series of dry years.

Landward a complete ring of the Chamaedaphne association has developed on the grounded edge of the mat. In a few places *Mariscus mariscoides* forms a small association between these two. It is especially interesting here, however, that in a few places the high bog shrub association is found ahead of the normal series of succession by invading here and there in the landward edge of the Carex mat between Carex and Chamaedaphne. The principal species is *Salix pedicellaris* and the invasion took place during the recent series of dry years while the Carex mat was temporarily grounded. Although not so well developed as at Smith's bog, nevertheless it appears to be making headway. Eastward from the lake this association is well represented by the *Betula glandulifera* consocies forming a dense mass of vegetation.

A normal Chamaedaphne ring, with but few secondary species is followed by a zone of aspen on the upland. A few seedlings and small trees of *Pinus resinosa* and *P. strobus* on the most protected side toward the road are significant, but fires have largely maintained the aspen elsewhere.

To the west there is a rather small extension of the East Lake bog across the highway. Here with so many more fires the vegetation of the bog outpost is a heterogeneous mixture of various bog elements, including pieces of Carex mat, patches of *Chamaedaphne calyculata, Spiraea alba, Calamagrostis canadensis,* and here and there a clump of the fireweed, *Epilobium angustifolium* and small trees of *Populus tremuloides*. As this small part is somewhat drained, it is to be expected that it would gradually be vegetated with aspens.

LITTLE LAKE 16

In a shallow drainage basin running somewhat NW-SE in the eastern part of Cheboygan County is a group of lakes, of which Little Lake 16 is the largest. The lake itself has alkaline water (pH 8), a well-formed false bottom, mostly about 15 cm. below the surface but towards the southwestern part as much as 1.4 m. down. The depth to the sand bottom over most of the lake is about 2.4 to 2.6 m. but in an area a little to the southeast of the center the depth is as much as 3.4 m.

Perhaps the most interesting thing about this lake is the presence of floating islands. The most mobile are those formed by *Juncus militaris* rooted in the organic mud a meter or more below the surface (Fig. 26). The plants project from 0.5 to 1 meter above

the water and from a distance appear to be *Scirpus validus*. The Juncus islands are usually in the south central part of the lake, but under stress of three or four days of strong southerly wind may get even to the north part of the open water. However, the normal northerly wind soon returns them to the south central in which the movement is apparently easier with the lower false bottom. For the first time, in 1941, plants of *Juncus militaris* were found rooted in muddy sand on the east shore where a small section of the mat was destroyed in putting out a small dock. The other floating islands are chunks of the mat from the west side of the lake, wedged off first by ice work and acted upon by wind. The most conspicuous perhaps are the islands of *Nymphaea odorata* which were a part of the west shore in 1936, a little separated in 1937 but by 1939 more than 15 m. out in the lake (Fig. 23). Chunks of the Carex-Cladium mat are constantly being broken off. Some of them are relatively large. Some of these have been worked across the lake and attached to the eastern mat. The very abundant waterlilies at the north end of the lake may have been augmented by such floating islands (Figs. 24 and 25).

Under the large mat surrounding the lake no depth to sand greater than 2.5 m. has been found, with the one exception of 2.75 m. close to the edge of the center of the west side of the lake. The mat is narrow on the east side of the lake but wide elsewhere. At the north and west sides of the lake the mat is about 40-50 cm. thick, floating over a semiliquid peat, with the lowest part of the peat rather firm for the lowest 15 to 20 cm. This quaking mat had as a starter *Carex lasiocarpa*, which is now quite largely overrun with *Mariscus mariscoides*, making a mat which is extensively humped in narrow ridges by ice. These ridges are the locale of invasion by bog shrubs, as Chamaedaphne, and even bog trees as Larix and *Picea mariana*. The Cladium association has several interesting secondary species, including:

Rynchospora alba, *Scirpus hudsonicus*, *Carex diandra*, *Triglochin maritima* and *palustris*, *Eriophorum virginicum* and *E. callithrix*, *Xyris montana* (only place in the region), *Utricularia vulgaris*, *Drosera* spp., *Scheuchzeria palustris*, *Lycopodium inundatum*, *Habenaria blephariglottis*, *Pogonia ophioglossoides*, *Calopogon pulchellus*, *Menyanthes trifolia*, and *Vaccinium macrocarpon* and *V. oxycoccus*.

Certain Sphagnums come into this mat, forming a low growth hardly above the water, but the higher Sphagnums come with the shrubs of Chamaedaphne soon after it arrives.

Farther away from the lake the Cladium mat with or without *Carex lasiocarpa* is grounded, with relatively solid, but not hard, peat beneath it, a distance of 2.45 m. from sand to the upper surface of the mat. Into this grounded mat *Chamaedaphne calyculata* quite generally invades and into the Chamaedaphne come *Larix laricina* and *Picea mariana*. Comparatively near the lake the individuals of Picea that started some years ago have now layered well, forming some beautiful specimens. These have escaped the ravages of fire which has completely burned off the Picea forest which formerly vegetated the entire area from near the lake to the pineland 0.4 to 0.8 km. or more away. Throughout the western part of the area, Chamaedaphne now holds sway. With it are numerous bushes of *Vaccinium canadense* and *V. pennsylvanicum* and in the hollows left after the Piceas were burned away, *Eriophorum callithrix* and *E. virginicum*. Into this large area just a few new *Picea mariana* saplings have come as seed invasions. The Chamaedaphne in this area was defoliated by larvae of a Geometrid (*Cingilia catenaria* (Drury)), over an extensive area in 1941, so much as to change the color of extensive tracts from green to the reddish brown of Chamaedaphne stems. Closer to the pineland, more ravages by fire have burned even Chamaedaphne out and an open vegetation of *Populus tremuloides* and *Scirpus atrocinctus* has sprung up, with occasional admixtures of the high bog shrub association.

Toward the southern part of this area some examples of bog trees much mixed with bog shrubs still remain. A short distance north of the lake a well developed Picea forest with trees more than 80 years of age remains free from the ravages of fire. Some Larix is present, but a sprinkling of Thuja indicates what can be expected in the future, barring fire. In this Picea is one *Pinus strobus* which appears to be about 24 years old.

In between the Cladium mat and the islands of Chamaedaphne there often appear a few representatives of the Iris association, such as *Eupatorium perfoliatum* and less frequently a few clumps of the grass, *Calamagrostis canadensis*, but neither in sufficient abundance for more than casual mention.

FRENCH FARM LAKE

South of the east end of Cecil Bay, separated from Lake Michigan by a series of sand dunes is the shallow lake known as French Farm Lake or French Lake, a rather ovate-shaped body of water bordered on the west by a narrow sandy-marly shore. In protected bays the aquatic Potamogeton and Nuphar-Nymphaea associations extend up on to the shore into a general Scirpus-Eleocharis association or end abruptly at the pine upland.

At the east end of the lake an extensive mat, 0.5 km. wide, completely covers the lake. At the frayed, iceworked, western edge this mat is about 40 cm. thick and floating over clear water. On the false bottom in front of the edge of this mat is a fine growth of *Scirpus subterminalis*, a bog plant found in only one other bog in this region.

Floating to half-anchored colonies of *Pontederia cordata* occur in this lake (Fig. 19). Pontederia is present in but one other bog lake in this region.

SUCKER CREEK DRAINAGE SYSTEM

Sucker Creek arising from Upper O'Neal Lake and flowing through Lower O'Neal Lake to Lake Michigan in Sturgeon Bay, a distance all told of about 5 km. is bordered by bog vegetation throughout. Width of

the bog vegetation varies considerably in different parts, but is widest at Lower O'Neal Lake.

UPPER O'NEAL LAKE

At the very head of the Sucker Creek drainage system is a small, shallow bog lake, completely surrounded by a bog mat, but with the center of the lake occupied by the *Scirpus validus* association rooted in marly mud at a depth of 50 to 150 cm. Submerged aquatics, as various species of Potamogeton and Myriophyllum occur among the Scirpus stems.

The mat is about 5 to 7 meters wide, floating at the lake edge. It is especially interesting in being one of the three places in the region in which *Eleocharis rostellata* is to be found growing.

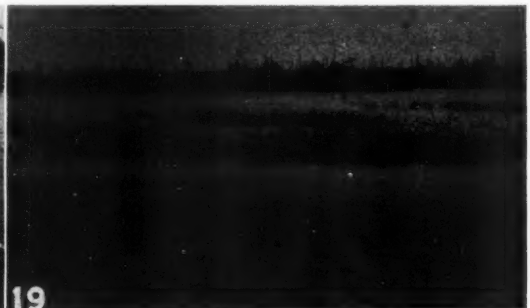
Landward the mat has been invaded by various bog shrubs, including Chamaedaphne and closer to the edge by the bog trees, Larix, Picea, and Thuja.

This lake is drained by a sluggish stream mostly lost in anastomoses through bog tree associations into Lower O'Neal Lake.

LOWER O'NEAL LAKE

A moderate sized, rather shallow bog lake, in the Sucker Creek drainage system, receiving water from Upper O'Neal Lake drains into Lake Michigan through Sucker Creek. When first studied, the lake had a wide mat on both sides of a fair-sized lake (Fig. 21). The mat was definitely, although lightly grounded on sand bottom about 1.4 meters down. Irregular holes in the mat gave ice a chance to work in the mat. Shoreward, invasions of bog shrubs were the rule, except in burned areas, where thickets of Alnus and *Populus tremuloides* were to be found. Transition to the pine woods surrounding was abrupt, except along the line of the streams, where bog shrubs, thickets of Alnus and Salix or bog trees were found.

A beaver dam, built in 1932, raised the level of the lake about 1.7 meters, somewhat reduced the amount of *Scirpus validus* and *S. acutus*, drowned out parts of the mat which remained attached to the bottom and all of the marginal bog and pine vegetation and floated up the floating and imper-



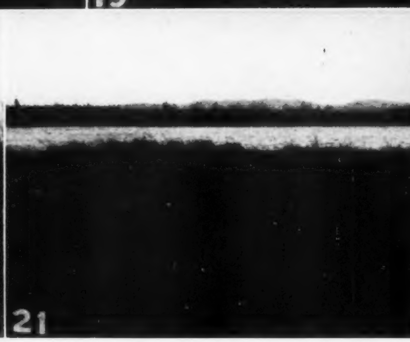


FIG. 18. The margin of Munro Lake showing an extensive development of the Nuphar-Nymphaea association on organic mud. A fringe of Typha in the left foreground is followed landward by a wide Chamaedaphne mat. (Photograph by Esther Rodger. August, 1935.)

FIG. 19. A view of French Farm Lake showing organic mud and semifloating mats of *Pontederia cordata.* August 8, 1925.

FIG. 20. A view of the region above the mouth of Maple River showing a Typha mat, *Fraxinus nigra* (with enlarged bases), in the foreground *Equisetum fluviatile, Bidens beckii* and *Carex lasiocarpa.* In the background the lowland forest of *Fraxinus nigra* into which many trees of *Thuja occidentalis* are invading. August 7, 1920.

FIG. 21. View of Lower O'Neal Lake showing the Carex mat growing out around *Scirpus acutus* of the lake. Bog woods in the background. August 4, 1932.

FIG. 22. The wide mucky marl mat margin at Wycamp Lake showing *Scirpus acutus* and the arching rooting culms of *Eleocharis rostellata.* August 1, 1929.

fectly attached masses of the mat, thus greatly increasing the area of the lake.

Although in a back part of the country and harming no one, this dam was dynamited out in the early spring of 1937, dropping the lake to the former level. However, the great growths of the floating mat and the rearrangement of mat masses by ice and wind resulted in 7 not too well defined, little lakes in place of the former single one. This was accompanied also by a notable increase in the amount of Scirpus.

The marginal vegetation was not re-established at all in 1939, but the prompt germination of a few *Pinus resinosa* seeds that fell on the mat, grounded near shore when the lake fell, has resulted in seedlings which were two years old and 20 cm. high in 1940.

WYCAMP LAKE

An irregular shaped lake, nearly 3 km. long and up to 1 km. wide, known as Wycamp Lake, drains into Lake Michigan north of Cross Village through a small stream about 2 km. long. The lake itself is mostly shallow (7.5 m.) with a sandy, marly zone mostly replacing a regulation bog mat. This zone may be several meters wide, but it is especially interesting in being the place where *Eleocharis rostellata* was first found in the region and remains the most extensive patch (Fig. 22). In this locality it is growing in marly muck along with *Scirpus validus*, but in Upper O'Neal Lake it is growing on a regular *Carex lasiocarpa* mat into which Chamaedaphne is invading.

The shore itself is either a marly muck, or an essentially sandy beach where ice work has been active. Back from the shore occurs either normal bog woods of Thuja, Picea, and Larix or in burned-over areas various mixtures of these with aspen and lowland forests.

CECIL BOGS

In the area adjacent to the former town of Cecil on Lake Michigan and again in the Grass bay area along Lake Huron are several small bogs, largely beach pool in their origin. All of them begin as shallow ponds formed behind shore dunes or ridges. One such is illustrated in Figure 27.

THUJA BOGS

There are many areas of Chamaedaphne and of Thuja in various stages of development, whose description would merely be repetition. Among them may be mentioned an area both sides of U. S. Highway 31 just north of the Bliss road crossing, north of Levering. It is excellent in showing the oncoming Thuja not quite yet as tall as the aspen which covered the ground after fires some time ago. Farther south, between U. S. Highway 31 and Arnott Lake, Thuja has eliminated the aspen and presents an excellent young Thuja association.

In addition to those lakes and bogs described, numerous others exist in the region. As they are similar to one or another of those described in the absence of detailed study, no further mention will be made of them.

THE PLANT ASSOCIATIONS OF BOGS

THE CHARA ASSOCIATION

In the deep water, to which sufficient light has access, plants of Chara usually form the initial vegetation in the waters of lakes or ponds, and may be succeeded subsequently by either bogs or swamps. Chara is, however, found more frequently in ordinary aquatic habitats, as streams or lakes or borderline habitats as beach pools, than in the bogs of this region. It sometimes forms large masses which have the appearance of large rocks under water.

In Douglas Lake, Chara may be found in water as much as 5.5 m. deep. Usually it is without associates other than algae, but at Hook Point *Isoetes braunii* Durieu occurs with it.

Into masses of Chara, species of Potamogeton come and finally replace it.

THE POTAMOGETON ASSOCIATION

More commonly the association initiating vegetation in bog lakes is the Potamogeton association, although, to be sure, this association is much more frequently and better developed in ordinary aquatic habitats. In the ordinary bog lake with its mat projecting out over the water, the depth to bottom is usually too great for the development of this association. It is consequently not expected in any but shallow bog lakes. Even there, however, it is quite infrequent, as the conditions of many such lakes favor the extensive development of organic mud. By completely shutting off the light, the mud prevents the development of Potamogeton except on the surface. Even there, however, it is never plentiful unless the mud layer is thin and grounded on sand, as in some of the beach pool bogs.

Represented by *Potamogeton heterophyllus*, the association is present in mud at Smith's bog and at Mud Lake bog, to mention two. Perhaps the best examples of this association in bog lakes are at French Farm Lake and in Silver Lake in Bryant's bog. In these places the association is dominated by *Scirpus subterminalis* rooting in organic mud 30 to 100 cm. below the surface of the water.

Considered as a whole, this association is neither a typical nor an important one in bog vegetation of this region.

THE NUPHAR-NYMPHAEA ASSOCIATION

The next association in the progress landward is prominent at the surface of the water (Figs. 3, 4, 18, 23-25). The plants are usually rooted beneath more shallow water than the Potamogeton when in competition with it. The leaves spread out on the surface of the water or mud, where with their long flexible petioles they rise and fall with the water level. The association is not an important one in

bogs. In bogs in which the lake is deep, it is usually impossible for this association to exist, even though it was present when the mat began to push out from the shore. In rare instances, especially if the mat is accompanied by considerable organic mud, the rhizomes of *Nuphar advena* or *Nymphaea odorata* may root in the mat and proceed out over the open water. However, if conditions are at all favorable for rapid development, the mat will overtake and surround the Nymphaea, thus making it a relic in the mat and presenting a mat front to the open water (Figs. 24 and 25).

At Little Lake 16, the Nymphaea association which had developed at the outer edge of the mat has now been separated from the mat by ice action. Since the organic mud under and around the Nymphaea is now sufficiently dense to hold the waterlilies up, this Nymphaea mat is floating slowly to and fro (Fig. 23). Three days of good wind in 1939 moved such a waterlily mat about 15 meters farther out from shore.

The Eleocharis Olivacea Association

An association of very restricted range in this region is present on the organic mud at Mud Lake (Figs. 6 and 7). The dominant species and for several years virtually the only species present is *Eleocharis olivacea.* When first noticed in 1916, the individual plants appeared on the mud without relation to other associations. In low water years the association carpets the mud with an olive green vegetation of low tufted plants. In years of high water the vegetation is rather sparse as the plant does not do well unless the organic mud reaches the surface of the water. In the early years there were no secondary species aside from a few plants of *Bidens cernua, Dulichium arundinaceum, Glyceria striata* and *Eleocharis* spp., but during the recent dry period on the firmer mud were more than a dozen species, including the above and *Leersia oryzoides, Calamagrostis inexpansa, Potentilla palustris, Scirpus atrocinctus, Epilobium adenocaulon, Lysimachia terrestris, Eriophorum* spp., *Carex* spp., and even a few plants of *Achillea millefolium.*

Since neither the *Carex lasiocarpa* nor the Chamaedaphne associations appear to invade the *Eleocharis olivacea* association on this soft organic mud, its successional relationships are not yet clear. In fact landward or rather matward, there is frequently an open water channel made by muskrats separating the main body of mud from the mat.

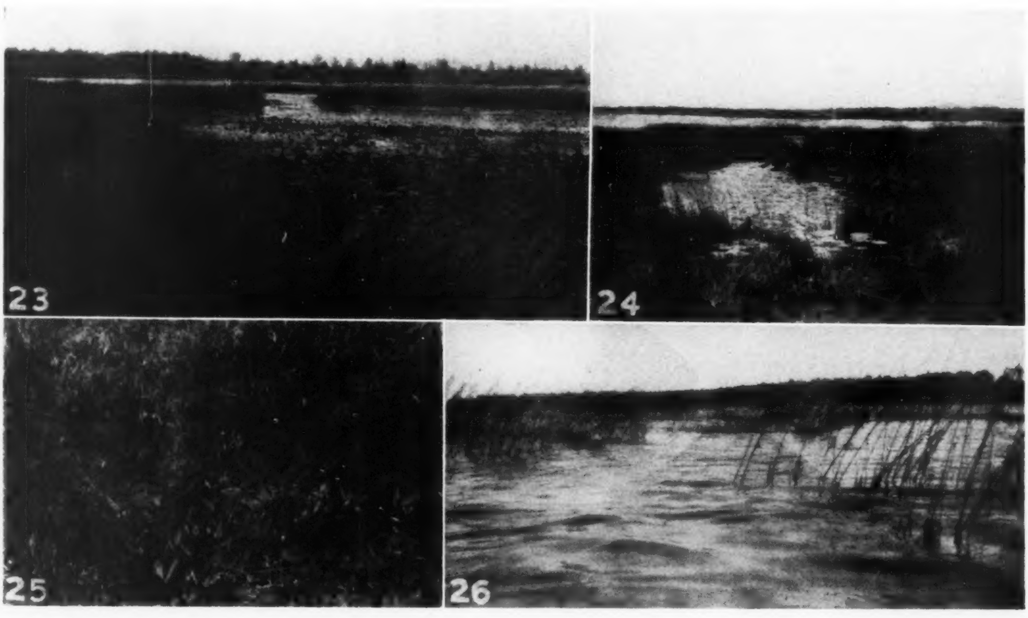


FIG. 23. The western edge of Little Lake 16 showing floating islands which have been cut off from the main sedge mat by ice work. These islands float at the mercy of the winds on the organic mud which reaches nearly to the surface. An extensive development of the Nuphar-Nymphaea association filled in the space in the center in a period of 3 years. (Photograph by G. E. Nichols. August, 1937.)

FIG. 24. The mat at the north end of Little Lake 16 showing how wind-blown floating mats of Mariscus and *Carex lasiocarpa* have cut off pools of Nymphaea. (Photograph by Marion Lehner. July, 1938.) (See Fig. 25.)

FIG. 25. A pool of Nymphaea such as shown in Figure 24 nearly obliterated by the invasion of Sphagnums and sedges. A few water lilies can be seen in the center. (Photograph by Marion Lehner. July, 1398.)

FIG. 26. The deep floating mats of *Juncus militaris* in the south center of Little Lake 16. August 5, 1937.

THE MENYANTHES-SAGITTARIA ASSOCIATION

In boggy areas in this region one of the associations of comparatively little importance is dominated in bogs by *Menyanthes trifoliata* (Figs. 16 and 17). As seen now, it is normally a relic in the *Carex lasiocarpa* mat or in open places in the Chamaedaphne association. However, it has been observed pushing out into the mud ahead of the *Carex lasiocarpa* mat provided the organic mud was sufficiently close to the surface. It thus forms a loose, thin, unstable assemblage into which *Carex lasiocarpa* or Chamaedaphne readily spreads and soon eliminate the Menyanthes.

Under swamp conditions, as at the mouth of Maple River in Burt Lake and in Indian River near its mouth in Mullet Lake, this association has proceeded out over open water along the edges of the channels, enveloping stems of *Scirpus validus* or *S. acutus* whenever encountered. Flowing water in summer and ice work in spring prevents any typical bog development, however.

A *Sparganium minimum* consocies existed under similar conditions in Smith's bog prior to 1929. When the mat in this bog first grounded, this association rapidly increased in extent for three years, then diminished and became entirely replaced by the *Carex lasiocarpa* association.

The presence of the association is frequently indicated by plants of *Potentilla palustris*, *Cicuta bulbifera*, or *Proserpinaca palustris*.

THE SCIRPUS VALIDUS ASSOCIATION

Although not an association expected in pure bog habitats, nevertheless the *Scirpus validus* association occasionally persists when bogs overcome lakes, especially shallow lakes. The dense mass of rhizomes of *Scirpus validus* or *S. acutus* are in the bottom in marly mud. They sink in the ordinary organic mud unless it is dense. With the latter condition a fair development of the *Scirpus validus* association is possible, but in a densely developed bog mat *Scirpus validus* can rarely maintain itself, let alone make headway.

At Lancaster Lake, where conditions are intermediate between open lake and bog, this association is somewhat better represented than normal with *Equisetum fluviatile* as a codominant. The association is also well represented in the beach-pool bogs in the vicinity of Cecil, where it is a relic of the time when these areas were a part of Lake Michigan. In Blanchard's bog a few culms of Scirpus have persisted for a long time in the mat. Their rhizomes are quite attenuated, sharper pointed, and the small number of "feeding roots" contrasts greatly with the heavy rhizomes and dense mass of roots of these species of Scirpus in the normal aquatic habitat. However, even in these bogs, it will sooner or later be eliminated by the shade of high shrubs or trees, if not earlier for some other reason.

At Lower O'Neal Lake, beyond the bog mat a somewhat sparse *Scirpus validus* association (25 to 50 culms per square meter) was rooted in marly mud 1 to 1.5 m. below the surface of the water. In the greatly enlarged lake following a beaver dam constructed in the spring of 1932 *Scirpus validus* began to lose out except as clumps of roots and rhizomes became loosened from the bottom and floated to a more suitable place. Dynamiting out the dam early in 1937 dropped the lake to its former level, regrounded parts of the mat which had broken loose, but allowed the organic mud under the mat to flow out into the former lake, mixing it freely with the marly mud. This readjustment of floating mats and masses of mud has made about seven smaller "lake areas" in place of the former single larger lake. In these lakes the mud and marl are at a higher level, even to the surface, and are much less dense. These conditions have favored a great increase in the area occupied by the *Scirpus validus* association.

THE SCIRPUS AMERICANUS ASSOCIATION

Another aquatic association, which is frequently extensive in and around lakes and streams, is decidedly rare in boggy areas. It merits scarcely more than passing mention because of the ease with which it is eliminated by a developing mat unless the water is decidedly shallow.

In shallow water on organic mud, as at Smith's bog, this association, represented by *Eleocharis palustris,* is between the Nuphar-Nymphaea and the *Carex lasiocarpa* associations. It is, however, being rapidly invaded by the Carex. It will disappear in a few more years if present trends remain operative.

Among the codominant species, *Eleocharis rostellata* is worthy of special mention (Fig. 22). This spikerush is unique among aquatic monocots of the region in taking root at the bent-over tip. Each stem ends in a terminal spike, which has a single bud at its base, as was pointed out by C. D. LaRue in his special study of vegetative reproduction of this plant (LaRue, 1935). In the "steril" culms, the flowers have aborted. The culms grow long, becoming about 2.5 times the length of the normal fruiting culms, arches over and roots at the tip. In Wycamp Lake and in one of the Twin Lakes, *Eleocharis rostellata* grows along the shore of the lake in stony soil soaked with water, but, at Upper O'Neal Lake a patch of this sedge, about 300 meters long, is at one end growing in stony soil of the lake bottom along with *Eleocharis palustris*, while the other end of the patch is rooted in a floating mat of *Carex lasiocarpa,* into which species of Sphagnum are invading. The water of this mat is slightly alkaline in chemical reaction. This is characteristic of the other habitats in which this plant has been found in this region, although experiments have demonstrated that the tips will sprout in conditions as acid as pH3.

THE CLADIUM ASSOCIATION

In beech pools in which bog vegetation is developing, this association of rushlike sedges is occasionally quite extensive, especially in the East Point region of Douglas Lake. The dominant species, *Mariscus mariscoides (Cladium m.),* forms a dense mat of roots

and rhizomes at the water table level. Its extinction results from the invasion of bog shrubs, especially *Myrica gale*.

At Little Lake 16, irregular patches of the mat to the north and northwest of the lake either belong to this association or are relics or admixtures of it (Fig. 23, left front). Here it is abundantly associated with *Sphagnum* sp., beneath which the organic mud is rather flocculent. Occasionally small colonies of *Lycopodium inundatum* are present on such loose mats and *Juncus pelocarpus* occurs at the edges.

The Phragmites-Typha Association

The Phragmites-Typha association of tall grass and cattails is present more frequently in the beach-pool type of bog where it may form a partial fringe just in advance of the shrubby zone at the margin. In many cases this is the zone of ice work and the disturbance in the original vegetation gives opportunity for this association to appear. In the usual bog habitats, the association represented by Typha is seldom present, but when found is usually in places which have been greatly disturbed either by fire or tramping (Fig. 18, left edge). Once established, it has the ability to spread to a certain extent in the mat, but in so doing it hinders the development of the mat. This results in a thinning of the mat and may even go so far as to render conditions unfavorable for the Typha itself, resulting in its elimination.

The Juncus Militaris Association

An association disjointed from others occurs in Little Lake 16. It is dominated by *Juncus militaris*, a rush which grows in water and has its roots buoyed up in the organic mud of the false bottom, usually at a depth of one meter or a little more. Above the water the stem projects about a meter (Fig. 26). From a distance the appearance is that of *Scirpus validus*, but this Juncus will grow on a more fluid or less dense organic mud mat than Scirpus is likely to do. Although not a great deal of the plant is exposed above the water, masses of individuals are at the mercy of the winds and such patches are slowly blown from one part of the lake to another. As the main part of *Juncus militaris* is about a meter below the surface the field of movement of this association is mostly limited to the southern part of the lake where the top of the organic mud or, in other words the false bottom, is deeper.

With the Juncus have been noted only submerged species, as *Myriophyllum* spp., *Potamogeton* spp. and a species of Sparganium with flaccid submerged leaves.

Occasionally a floating mat of Juncus comes in contact with a floating mat of waterlilies, but the much more mobile Juncus patch does not seem ever to attach to the waterlily mat, so far as observed. In 1941, for the first time in this region, a small patch of *Juncus militaris* was found rooted in the muddy sand of the shore where the mat had been broken up at a place where a small dock had been built several years previously.

The Calamagrostis Association

The Calamagrostis association of wet-meadow grasses occurs in many places in the region on wet ground. Although not normal to the bog habitat, it has invaded it in a few places, both in the beach-pool bog type of habitat and in the margins of strictly normal bogs. The invasion has usually followed fire which has burned out previous vegetation. Under conditions of relatively low water, seeds of *Calamagrostis canadensis* germinate readily and frequently establish this association. Although Calamagrostis will stand a good deal of wet ground, if later the area is too persistently flooded, the plants of Calamagrostis first show difficulties in their water relations by the development of anthocyanin color and disappear entirely. At Smith's bog where low water conditions have obtained for many years after the inception of this association, it has not only proceeded to normal development but has encroached upon the *Carex lasiocarpa* mat, making headway at the rate of from 10 to 30 cm. a year. Whether the wetter years that are due will reverse this succession remains to be seen.

When wooded bogs are cleared, usually by burning, the Calamagrostis association may become established in irregular patches here and there as part of the revegetation of such areas. Its existence, however, is transitory unless fires are repeated, as shrubs and trees come on so quickly in the wet ground.

In this region this association is dominated most frequently by *Calamagrostis canadensis* and less frequently by *Calamagrostis inexpansa*, occasionally both in the same area.

The Iris Association

This association of herbaceous plants is frequently present at the margin of the herbaceous vegetation and the shrubby vegetation both in normal bogs and in beach-pool bogs. In the former the development of the association is less extensive, both as to areas of ground covered and number of species usually present, than in the latter. In bogs it may be but a mere fringe of Iris less than 30 cm. in width, but more frequently it is represented by *Dryopteris thelypteris* which has not wholly supplanted the Carex. In beach-pool bogs the association is frequently quite well developed, forming a fairly broad zone at the margin of the wet area, even extending up onto the shore a short distance. While Iris is usually the outstanding species, in autumn several showy composites attract attention, noticeably *Eupatorium purpureum*, *Eupatorium perfoliatum*, *Bidens cernua*, and *Solidago uliginosa*, while in midsummer *Lysimachia terrestris* is conspicuous. Most of the plants are rhizomatous plants and compete beneath the surface of the ground. They will stand all ordinary flooding and are also able to stand withdrawal of the water for fair periods.

This association gives place to associations of woody plants, among which its members often remain for several years as relics.

THE CAREX LASIOCARPA ASSOCIATION

This association of sedges may follow any one of several strictly aquatic associations of emersed plants or it may start at the edge and project out into the water (see Figs. 3, 5, 6, 7, 8, 13*, 15* and 21). It is here perhaps the most important of the associations in the filling up of bog lakes and in initiating the formation of peat. In the Douglas Lake region, this association is present in nearly all of the bogs as well as in certain beach-pool bogs and occasionally along streams. Usually it forms a border or circumarea around lakes. Smith's bog presents a remarkably fine example of an extensive development of this association (Woollett, Dean, & Coburn 1925). Here the association covers an area of about 23,000 square meters in which there is scarcely another plant in addition to *Carex lasiocarpa*. The mat formed there is nearly a meter in thickness and has only recently become grounded (1921). With the grounding, quaking is no longer present. In Mud Lake bog the quaking mat does not exceed 60 cm. in thickness, but here also the quaking is becoming less due to the extensive development of organic mud.

The dominant species, *Carex lasiocarpa*, grows from rhizomes which do not decay readily, but form extensive mats of vegetation. At first this is a ground association bordering the area, but as it develops it projects out into the water and makes the floating mat so characteristic of early stages of bog development. The long slender leaves and flowering stems appear from 0.3 to 0.5 of a meter above the surface of the water. As growth proceeds year after year, dead portions of the mat sift down and cover the bottom of the depression. This should lead ultimately to the building up of the bottom to within reach of the mat unless there are water currents which carry away the material as fast as it falls. Such a process of course leads to the extinction of the lake. Such building up sooner or later brings the roots of the Carex too near the surface, under which conditions succession rapidly replaces the Carex association.

The leaves of *Carex lasiocarpa*, being very slender, cast but little shade. This is clearly evidenced by the absence of shade leaves on Chamaedaphne plants invading the mat.

Once started, in the absence of wave action or ice cutting, the association covers the lake in a relatively short time limited only by its rate of vegetative growth. Wave action hinders this development by breaking up the edge of the Carex mat and pushing it up where it dries out and dies. Ice action, unless it can push into the mat, is usually not so important, as the mat is below the surface of the water. Ice forming at the surface depresses the mat somewhat and so prevents the upheavals that would result in the death of the Carex. When the mat is built up to such a thickness that the surface of the mat is close to or at the surface of the water for any length of time during the season, invasion is certain to begin. Invasion once accomplished ecesis usually proceeds rapidly, resulting in the early replacement of the *Carex lasiocarpa* association, which cannot withstand shade and can withstand being at or slightly above the surface of the water only in the absence of competition. In bogs the association which usually follows is the Chamaedaphne association. There are many instances of this succession in this region, but any other shrub association invading the *Carex lasiocarpa* will quickly replace it. The most frequent examples in the Douglas Lake region are associations dominated by *Myrica gale, Salix pedicellaris, Salix* spp., *Cornus* spp., *Aronia* spp., or *Alnus incana.* Such are most likely to occur around the edges of the bogs and not on the mat itself, unless the mat has become grounded. No instances are at hand of tree associations directly invading a *Carex lasiocarpa* mat without an intervening shrub stage.

As one sees an expanse of *Carex lasiocarpa* association from year to year he has an impression of sameness that figures of density taken in different years belie. At the close of a period of very dry years in 1938, however, it did seem even from casual observation that the stems were farther apart. The following table shows how different the situation may be in different years. At the same time that the number of culms decreases per square meter, the diameter of the individual culms increases, but as shown in the same table not in any regular proportion.

TABLE 4. *Carex lasiocarpa* in Smith's bog and at East Lake.

Year	Character	Culms per square meter	Av. diameter in mm.
		Smith's bog	
1932	dry	298	2.4
1935	wet	431	—
1936	dry	346	—
1937	moderately wet	285	1.4
1938	dry	192	5.1
1939	wet	435	3.23
		East Lake	
1940	wet	481	2.32
1941	dry	259	2.57

In each case at least 20 square meters were counted and at least 400 stems were measured.

Secondary species in a *Carex lasiocarpa* association freely floating as a mat are few and far between. They include *Carex stricta, Juncus canadensis* and *Dulichium arundinaceum.* Associated also may be a few relic species, as *Eleocharis palustris, Nymphaea odorata, Potamogeton heterophyllus, Potentilla palustris,* where this assocition has been preceded by others.

As the mat becomes more and more grounded, or as the organic mud fills the water under the mat and becomes sufficiently dense to raise the mat above a true floating position, the number of secondary species increases, likewise the instigation of active invasion. In addition to those mentioned above, the following are most frequent: *Carex sterilis, Eriophorum virginicum, Glyceria borealis, Hypericum virginicum, Lysimachia terrestris,* and the terrestrial form of *Polygonum amphibium.*

Invading species most frequently appearing are *Chamaedaphne calyculata, Andromeda glaucophylla, Sphagnum* spp., *Salix pedicellaris, Iris virginica, Calamagrostis canadensis,* and *Alnus incana.*

By the time the mat has become thoroughly grounded invasion sets in rapidly and it takes but a few years for Chamaedaphne to spread over the mat. Fires assist this materially.

In most of the bogs of this region the conditions favoring invasion, in the past, have been so pronounced that but narrow mats of *Carex lasiocarpa* with frequent indication of ice work on the outer margin are found. In Smith's bog alone there is a wide mat of *Carex lasiocarpa* but even in this bog the successional changes rampant during the past drouth cycle have materially cut down the expanse of pure *Carex lasiocarpa.* At the present rate and under the present conditions, the *Carex lasiocarpa* stage may not exist for more than 20 years.

During the past 16 years, *Carex stricta, Carex sterilis, Hypericum virginicum,* and *Lysimachia terrestris* have been increasing as frequency indices in order indicate 8 to 46, 11 to 46, 2 to 16, and 6 to 28. *Juncus canadensis* has maintained a frequency index in the forties throughout the period, while *Dulicheum arundinaceum* has dropped from in the fifties to below 10 and *Potentilla palustris* from 11 to 5. Sphagnum has made its appearance in a few spots but nowhere yet in any quantity.

The mat at East Lake is second best. However, it is grounded and invasion by the Cladium association is active.

The Sphagnum Association

While species of Sphagnum for the most part in this region are secondary species in the bog-tree association or codominants in the Chamaedaphne association, in parts of the Mud Lake bog and the Little Lake 16 bog, certain species of Sphagnum have invaded the *Carex lasiocarpa* mat ahead of Chamaedaphne or filled over open patches of water in the mat. The Sphagnum may surround waterlilies, modifying their structure, if any are present, or cover over the false bottom of organic mud.

Such areas of Sphagnum may be overrun by the *Carex lasiocarpa* association, but are more likely to be overrun by cranberries, *Vaccinium oxycoccus* or *V. macrocarpum,* invading members of the Chamaedaphne association, before Chamaedaphne itself arrives in force. Sooner or later the areas become dominated by the Chamaedaphne association.

The Salix-Cornus Thicket Association

This association of shrubby plants found in many wet ground conditions in the Douglas Lake region is present to a limited extent around the edges of certain bogs and along roadways cut through bogs. While the association withstands short periods of submersion, complete inundation of the roots and lower parts of the stem throughout the year is not favorable to the development of the association unless in an aerated spot or in the virtual absence of competition with more natural bog species. As soil conditions seem to have no part in the location of this association, the highly organic bog muck may support a vigorous development, particularly of *Salix discolor, Salix bebbiana,* and *Cornus stolonifera,* belonging to this association. Of these the species of Salix are much the more frequent in bogs. The usual growth of these shrubs forms an arching canopy over the ground which kills out the more typical bog plants and to a certain extent causes the breaking up of the mat in between the shrubs. In these interstices there may be secondary species of many different types but in considerable quantity only if the bushes are well spaced. The marginal fosse is a very likely place for the appearance and persistence of this association from which it may spread out to a limited extent onto the mat, as at Smith's bog, especially when the mat has become grounded. Landward this association is eliminated by the invasion of trees.

In one particular area near Ingleside where a bog forest was cut and the land sowed and used for pasture, a very high water year (1917) killed out the pasture grasses. Within a couple of years this area became overgrown with species of Salix and by 1923 was a mixture of Salix and Cornus as viewed from the outside but as one walked through it he saw a mixture of various grasses in the open places in between the bushes with here and there a seedling tree of *Acer rubrum* or *Fraxinus nigra.* By 1926 these tree seedlings had grown higher than the bushes of Salix and Cornus and the area is now a lowland woods into which seedlings of Thuja have invaded. In time Thuja will dominate the vegetation.

In nearly every case of the development of the Salix-Cornus thicket, there has been interference by man with the primeval conditions and the Salix-Cornus thicket is not expected to remain unless disturbance is kept up. Salix-Cornus thickets may be replaced by almost any species of the high bog shrub association or by the trees of the various bog tree associations.

The Chamaedaphne Association

The Chamaedaphne association is the most extensive bog association in the region (see Figs. 3, 5, 9, 12* and 13). It occurs in virtually every bog in the region and usually in large quantity. In some bogs the area is almost exclusively a pure stand of Chamaedaphne. Such is the case most prominently in Gleason's bog, Gates' bog, the eastern part of Mud Lake bog, the northwestern part of Vestal's bog, Malone Lake bog and until very recently in Bryant's bog. In the formation of peat this association is second in importance only to the *Carex lasiocarpa* association. In general appearance the association is a dense stand of low shrubs seldom exceeding about 80 cm. in height, covering the ground with a solid canopy. The stems vary in thickness from 1.0 to 12 mm., mostly between 3 and 5 mm. They are not usually over 4-5 years old. The oldest found was 11 years

of age. Although the number of stems per square meter varies greatly because Chamaedaphne grows in clumps, about 200 per square meter is common. Depressions mark the boundaries between the different bushes of Chamaedaphne. The association is normally present on the mat which has grown out over the surface of the water and, if it is to remain a pure association, the mat must not rest on the bottom of the depression. The association does not readily extend out into open water because the plants of Chamaedaphne are slightly heavier than water, consequently must be held up. This buoying up is done by remnants of the mat previously formed by *Carex lasiocarpa*. In situations most favorable to Chamaedaphne, but unfavorable to *Carex lasiocarpa*, the Chamaedaphne may spread over the Carex into the open water. There it forms an overhanging mass of shrubs which develop vigorously but do not extend much farther out into the water. If their support is too inadequate, they sink and add to the debris at the bottom. Such examples most frequently follow severe fire from which Chamaedaphne usually recovers quicker than Carex, or in the case of Bryant's bog the human interference with the sedge mat edge has been a serious factor in keeping back the development of the *Carex lasiocarpa*.

The root system of Chamaedaphne is shallow and composed of very few fibrous roots considering the fact that it is growing in water not readily available. The author's experiments (Gates 1914) have indicated, however, that in its usual habitat this root system is sufficiently adequate during the summer, but doubtfully so during the winter. Mycorrhizas are not associated with the roots as is the case with many bog shrubs. If unprotected during the winter, the tops generally are killed. Even in the absence of winter killing, the weight of the stems bears them down so that the bushes do not grow indefinitely in height. No Chamaedaphne plants exceeding 1.3 meters high have been found in this region. The plants are evergreen. When shaded the leaves grow larger and thinner than when growing in full sun.

While about 96 percent or more of the dominant plants in the association are *Chamaedaphne calyculata*, a few others are worthy of special mention. Four heaths, *Andromeda glaucophylla, Kalmia polifolia, Ledum groenlandicum* and *Vaccinium oxycoccus*, are quite characteristic but seldom conspicuous. Among herbaceous plants the most striking include the pitcher plant, *Sarracenia purpurea*, the sundews, Drosera, a few species of orchids, *Scheuchzeria palustris* and several species of Carex.

In newly developing conditions, the Chamaedaphne association will seldom invade anything but the *Carex lasiocarpa* mat. Once established on the mat, the plants spread vegetatively rather rapidly, forming clumps. As long as the mat is freely floating, the development of Chamaedaphne goes on slowly, but once the mat becomes grounded by the accumulation of debris and gelatinous muck so as to lift the mat somewhat from under the water, Chamaedaphne spreads very rapidly. This has been the case at Bryant's bog and is now becoming the case at Smith's bog where the shallowness permitted the development of a waterlily zone rooted in the Carex mat. In a few places the Chamaedaphne has been buoyed up by waterlilies and spread out into the open water of the small pond. With the filling up of the pond with organic mud, parts of these bushes of Chamaedaphne have been broken up by ice and spread around in the area. This is making the development of Chamaedaphne in this bog go on much faster than would usually be expected. In Smith's bog, as well as in other bogs of the region, Chamaedaphne becomes established on logs which have fallen into the bogs. It spreads along such logs and from them into whatever vegetation may be present; or even in extreme cases over some open water, especially where the organic mud is close to the surface.

The widespread distribution and abundance of Chamaedaphne in the Douglas Lake region where the bog type of soil would naturally be covered by the Thuja association, can easily be explained by the fact that the fires in the past have burned off the tree associations and to date Chamaedaphne has been more efficient in revegetating burned areas than have the trees. Further, the stems of Chamaedaphne matted in the debris around the bases are not usually burned sufficiently to be killed, whereas the trees present in such areas have to come from seeds. Stages in the extension of Chamaedaphne at the expense of the trees have been studied in the eastern part of the Mud Lake bog and at Gleason's bog, although they are present in many other places.

Following the Chamaedaphne association one expects either a high shrub type or trees. In either case succession is by woody plants which will root in a soil composed almost exclusively of organic matter. The high bog shrub association represented by *Nemopanthus mucronata, Salix pedicellaris, Aronia* spp., *Alnus incana* or *Betula glandulifera*, is the usual successor in the various bogs of the region. In the beach-pool bogs the Myrica gale association follows rather more frequently than other associations. This replacement of the Chamaedaphne can be seen admirably in different bogs of the region, but the best example is that of the replacement of the Chamaedaphne by Nemopanthus which took place in Bryant's bog. In 1917 it was first noticed that young plants of Nemopanthus were in evidence throughout the Chamaedaphne zone, although nowhere exceeding them in height. During succeeding years these small plants of Nemopanthus continued to develop, finally coming up to the height of Chamaedaphne in 1922, at which time the yellowish green of Nemopanthus began to contrast sharply with the darker green of Chamaedaphne. Once up in the light, Nemopanthus has developed extremely rapidly. In 1926 from the outside, one had an impression of a Nemopanthus association; but as one entered the area, it was obvious that Chamaedaphne was not as yet replaced. The development of shade characteristics in the leaves of Chamaedaphne, however, was proof that the replacement was on its way.

At the present time (1941) this succession has long ago been accomplished.

Among the tree associations that may follow, Larix is the first to consider, but in this region is now the least common. The intolerance of Larix and the excessive depredations of sawfly larvae are potent factors. In bogs in which the mat is not very thick nor well grounded, *Picea mariana* is now the usual successor, but ultimately with a development of a well-grounded firm mat the Thuja association, the climax bog association of the region, should obtain. Usually a Thuja stage, however, is reached through intermediate stages and not directly in most bogs of the region. In beach-pool bogs, Thuja has the best chance of succeeding directly. Examples of this may be seen at the bogs around Cecil.

Fires or burns in Chamaedaphne areas are sometimes so severe as to burn the humus material down to or even below the normal water level. Some such instances have made conditions favorable to the establishment of a Salix-Cornus thicket which normally means the practical elimination of the Chamaedaphne association. Ordinarily burned areas may support a growth of fireweeds, particularly *Epilobium angustifolium*, for a year or two, replaced in the second or third year by extensive development of Marchantia in and among small rejuvenating plants of Chamaedaphne. In the year following, a growth of species of Eriophorum which when extensively developed and when in blossom makes an appearance very similar to a cotton field in fruit (Fig. 29). By this time the Chamaedaphne has grown high enough to be dominant and from then on holds sway until something happens to prevent. It is also possible for aspens, especially *Populus tremuloides*, to develop in burned over Chamaedaphne areas. If such conditions are present, the establishment of a lowland aspen growth makes the chances of Chamaedaphne completely redeveloping virtually nil. Sometimes the Chamaedaphne rejuvenates more quickly than the aspen seedlings develop. In such a case Chamaedaphne continues to control. The occurrence of periodic fire is favorable to the maintenance of the Chamaedaphne association.

THE MYRICA GALE ASSOCIATION

The *Myrica gale* association, a community of low bushy shrubs about a meter or a little more in height in the Douglas Lake region, is partial to beach-pool bogs rather than to the ordinary boggy areas as distinct from lake basins. One can perhaps scarcely see why this association should be so limited in the

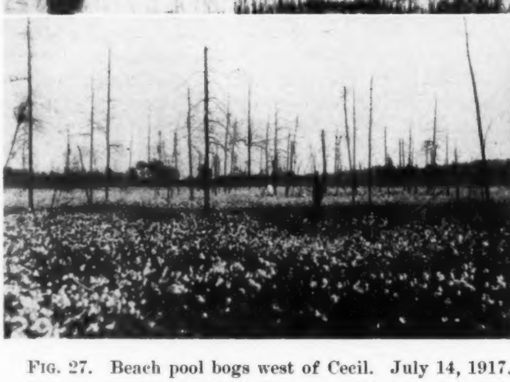


FIG. 27. Beach pool bogs west of Cecil. July 14, 1917.

FIG. 28. Penny marsh, a former forested bog from which frequent fires have removed all trees. The present vegetation is largely *Scirpus atrocinctus* with a riot of *Agrostis scabra* the year after each fire. August 9, 1934.

FIG. 29. View near the east end of Mud Lake bog. The *Eriophorum viridecarinatum* stage the second year after a severe fire in the Chamaedaphne-Picea association. July 20, 1918.

FIG. 30. A view of the interior of a well-developed Larix association northwest of Ingleside, showing density of the ground and shrub vegetation. July 19, 1925.

region, especially as *Myrica gale* is favored by the possession of root nodules containing nitrogen fixing bacteria in a soil in which nitrogen is very deficient. The species usually present include besides *Myrica gale*, *Salix candida*, and *Salix pedicellaris*. The other species present both of low shrubs and herbaceous plants are species not closely restricted by environmental factors and thus are able to develop in a wide variety of habitats. Many such occur quite abundantly in the Iris association. The association may follow Mariscus (Cladium) which it replaces by smothering its root system as well as by shading the aboveground parts and the Chamaedaphne association which it shades out. It is usually followed by the high bog shrub or the Larix association and in at least one case by the Thuja association directly.

THE HIGH BOG SHRUB ASSOCIATION

The area covered by high bog shrubs in the Douglas Lake region is very much less extensive than that covered by the lower shrubs (Figs. 4, 8 and 13 background). This is partly due to the fact that the trees encroach so rapidly on the high bog shrubs that in a place where they would get a chance to develop extensively the trees can grow also and eliminate the former. The species that are most likely to be present include *Aronia* spp., *Nemopanthus mucronata*, *Salix pedicellaris*, *Betula glandulifera*, and along more marshy areas with a slight drainage, *Alnus incana*. The association can survive within a wide range of environmental conditions, but the area actually covered is determined by competition with adjacent associations. The shrubs which compose it vary in height from about 1.5 to as much as 3 meters. Only shade-withstanding plants grow on ground between the bushes. Many of such species are holdovers from previous associations.

The association for the most part follows the Chamaedaphne association in which high bog shrubs start either in the shade or in open spots. By their shade they cause the Chamaedaphne to develop only shade leaves. As the shade of the high bog shrubs becomes still greater Chamaedaphne is eliminated. Such relationships are admirably shown at the Mud Lake bog and at Smith's and Bryant's bogs and more or less in most of the bogs of the region. In the beach-pool areas where this association occurs, it is more likely to follow the Myrica association which it replaces by shading.

As the association opens up the ground conditions, it makes conditions favorable to the development of such tree seedlings as can withstand its shade. The trees that usually follow are *Picea mariana*, or Thuja, but Larix may sometimes invade this association. Following a fire Larix may enter as long as the regenerating shrubs are too small to shade it, or it may invade areas in which the high bog shrubs are so widely spaced as not completely to shade the ground. The lowland forest may in certain places also replace the high bog shrub association, or in other places a few trees of *Pinus strobus* indicate that a pine association may develop.

THE LARIX ASSOCIATION

Among the tree associations widely distributed in the circumpolar regions of the earth, the Larix association is prominent in boggy areas. Formerly it was abundantly represented in the Douglas Lake region, but now, partly on account of lumbering and fire, but more particularly on account of the continued depredations of sawfly larvae (*Lygaeonematus erichsonii*), has well nigh vanished from the region as an important association. The association consists typically of a fairly dense growth of a deciduous coniferous tree, *Larix laricina*, a rapid growing, short-lived, conspicuously shade intolerant tree (Figs. 5, 8 and 30). For this association to start, its seedlings must be in open ground as the amount of shade that they can withstand is quite limited. In places where the inception of this association has been observed there has often been a dense stand of Larix seedlings in burned over or otherwise disturbed boggy areas. If Larix seedlings get the start and keep it, the Larix association will develop. This may take place on the upland as well as in boggy areas, but usually the upland conditions are so much more favorable for other trees that the Larix association seldom becomes established. One such place, however, is present on a ridge west of Lancaster Lake. The associated plants in this case are typical of an aspen community. As the trees of Larix lose their leaves during the winter, they can better withstand the drying effects of the winter winds at a time of year when their water supply is deficient. Since the trees are deciduous a great amount of light can get to the ground at least in early spring and until the canopy is established. Unless the trees are growing very close together even when in leaf, much light penetrates to the ground. This light is advantageous to a large number of secondary species, both among shrubby plants and herbaceous species (Fig. 30). A fully developed Larix association has therefore a large species list, although all the plants present may not be entirely typical of Larix as an association. Many of them grow indifferently in somewhat shaded areas on wet ground. The root system of Larix is very shallow. This fact together with the lack of density usually found in the association give the wind an excellent chance to topple over trees. The result is that old trees of Larix are seldom present. The oldest trees found were 130 years old. They were growing in a group in the forest surrounding Blanchard Lake. Windfall is thus a very common characteristic of the Larix association.

The Larix association may invade any association in which there is light sufficient for its seedlings to develop. The usual case is in the open spaces between the bushes of Chamaedaphne or Myrica, seldom on a Carex mat unless there has been a fire. The association is not very proficient in eliminating plants above which it grows as the trees of Larix are not close together nor is the shade they cast very great. Only tree associations which can shade it follow the Larix association. The usual ones are the *Picea*

mariana association on very boggy habitats, or the Picea-Abies association occasionally on less boggy habitats, or most commonly the Thuja association. In this region it appears that 50 to 60 years is the normal duration of a Larix association. Sawfly depredations have cut this figure down to such an extent that several former Larix associations have been succeeded by other forests within about 30 years. In view of these facts, the Larix association at the present time is rapidly becoming an unimportant tree association in the bogs of the region.

The Picea Mariana Association

The *Picea mariana* association is a common enough bog tree association in the northern part of North America, but in the immediate vicinity of Douglas Lake it is only sparingly represented in Bryant's bog, Livingston bog and in the Mud Lake bog. There is evidence of its former more widespread occurrence in the region, but fires have been the cause of its present restricted distribution (Figs. 6, 7 and 27).

In the low boggy areas at the eastern edge of Cheboygan County are still extensive developments of *Picea mariana* in areas more protected from fire. The best of these is that to the northward of Little Lake 16, but even at this lake there exists a much more extensive area from which *Picea mariana* has been burned out within the past 20 years. In most of this area the trees have been completely burned up, but sufficient territory remains in which the trees were merely killed and have not yet decayed sufficiently at the base to fall over, to give adequate proof of extensive distribution.

The association develops on a grounded mat and forms a tree cover of small spire shaped trees, seldom over 6 or 7 meters in height, seldom over 55 years of age. Old age is never the cause of the death of *Picea mariana*. Either attack by the dwarf mistletoe, *Arceuthobium pusillum*, lethal conditions set up by the free layering, or fire are the cause of death. Infestations with the dwarf mistletoe are particularly a serious handicap. Details of infestation are still a problem awaiting patient study and experimentation.

The seedlings of *Picea mariana* normally make their appearance in the Larix association and replace it by shading. This they may do in as short a time as 25 to 35 years, barring accident. Seedlings may also be present in the Chamaedaphne association, although they are perhaps more frequently present in areas of Sphagnum into which Chamaedaphne is also appearing. Mud Lake bog and the west side of Little Lake 16 are excellent examples of this condition. Its invasions into the *Carex lasiocarpa* mat directly are unusual and the few that have been noted have been on grounded mats. The Thuja association is the only one that follows the *Picea mariana* association. The secondary species that are found associated with spruce in this region are seldom characteristic of it, but are rather general to wooded bog habitats.

The Thuja Association

Nearly all the boggy parts of this region are or theoretically are likely to become covered with this association of conifers. The land that they occupy is low, water-soaked or very nearly so, cold, and consists almost entirely of organic matter. The association consists of coniferous trees such as *Thuja occidentalis* 71 percent, *Picea canadensis* 2 percent, *Picea mariana* 6 percent, *Abies balsamea* 7 percent, *Larix laricina* 3 percent, together with a few deciduous trees such as *Acer rubrum* 0.5 percent, and *Fraxinus nigra* 2 percent. The trees, especially Thuja, form a nearly impenetrable jungle of tough wiry branches. When fully developed, the shade is so dense that no ground plants occur. Fallen trees are frequent on account of the shallow root systems. These do not decay readily because of the coldness and the preservative qualities of the bog soil water. The ground is covered with needles, twigs and general debris, all in a slow stage of decay. Spots where light can reach the ground, as in openings between trees or where trees have fallen, are the habitat of quite a number of ground plants representative of many different genera. The association is dependent upon the maintenance of rather wet ground and as soon as the ground becomes drained or a slope is encountered, the association is replaced by upland types. This succession usually takes place in spite of the fact that Thuja itself can grow under upland conditions. The conspicuous exceptions occur within the moist air zone along the larger lakes, where Thuja may survive for several years.

Among the secondary species are several which are very typical of the association, including particularly the following: *Actaea rubra, Carex* spp., *Chiogenes hispidula, Cypripedium parviflorum, Equisetum sylvaticum, Habenaria* spp., *Mitella nuda, Moneses uniflora, Pyrola asarifolia, Rubus triflorus, Streptopus amplexifolius* and *Viola pallens*. As a majority of these species grow only in moderately dense shade, they have little or no value in controlling the habitat and consequently are of special interest only in the description of the association. Along roads almost any kind of plant that will grow in reasonably wet places is likely to be found if one explores the different roadsides carefully enough. Further, various species indicative of former associations that can withstand the shade of Thuja or which can maintain their growth above it, will persist for a considerable length of time.

This association can replace any bog association which is growing on firm soil, that is to say the Thuja association does not proceed out onto the mat of *Carex lasiocarpa*. In case seedlings do start on the landward border of the Carex mat, they grow exceedingly slowly and are not likely to establish a wooded area. The association invades by the development of seeds and young plants which grow under various conditions of light and by their shade at all times of the year eliminate other species. In the Douglas Lake region the Chamaedaphne association

is the one which Thuja is most likely to follow. In a complete genetic series, there should be intervening steps but these are often absent. Where intervening associations do occur, Larix will be readily followed by Thuja as will also *Picea mariana*. Among the shrubby plants the high bog shrub is normally followed by the Thuja association. The Myrica association at East Point, likewise is being succeeded by Thuja.

Outside of the strictly boggy conditions along beach pools the Thuja association sometimes replaces the Salix-Cornus thicket and transforms the area into a bog in place of the merely soggy moderately drained beach-pool condition.

In low dune areas along Lake Michigan where the atmosphere is moist nearly all of the time, Thuja grows readily on sand dunes, apparently a different type of habitat. Investigation usually discloses that the seedlings began at the edge of a beach-pool and continued to grow upward with the development of the dune.

The Thuja association is the climax association in boggy areas in the region. Without change of climate, as long as the boggy area persists without accident Thuja should remain as the vegetative cover. If, however, changes of the environment by the addition of soil material blown or washed in or a lowering of the water table level converts a bog into an upland area, upland associations gradually find their way in, in spite of the somewhat boggy conditions that remain. The ultimate outcome, barring accidents, should be the elimination of the bog altogether by upland vegetation. This is now taking place in certain areas in the region; for instance the area northwest of Reese's bog proper near the terminal moraine and, to a more limited extent, areas in the vicinity of Bryant's and Mud Lake bogs. In the first of these instances, soil borings have shown that the area has been very favorable for the development of peat, but at the present time at the surface little or no peat is being formed.

Secondary Associations

While the secondary successions resulting from fires are very apparent in this region, those on bogland are somewhat less conspicuous in comparison with those on the upland. This is principally because the boggy habitats have been able to recover from lumbering and fire sooner and so now present associations more like those which were removed. In a number of places a lowland forest of deciduous trees bids fair to be an important part of the area in place of the original Thuja. This has been particularly so in stream deltas. Elsewhere, however, conditions indicate that even the well-developed lowland forest will soon be replaced by the Thuja association.

Lowland Forest Association

Wherever boggy or wet ground has been cut over or burned over there is a possibility of the development of this association of deciduous trees, dominated most commonly by *Fraxinus nigra* (Fig. 20) and *Acer rubrum* (Fig. 31). Its general appearance and habitat relationships are very similar to the Ulmus-Acer association which is abundant in the central states. The striking differences are that *Acer saccharinum* in this region is limited to the ice ridge around Douglas Lake and that *Ulmus americana* is here more frequently found in the maple-beech forest than in the lowland condition.

FIG. 31. The lowland forest adjoining Bessey Creek near Douglas Lake featuring *Fraxinus nigra, Acer rubrum* and the fern *Onoclea sensibilis*. (Photograph by W. E. Praeger. August, 1918.)

The association maintains a growth which seldom exceeds 9 to 11 meters in height as the trees are not deeply rooted. Only rarely when *Ulmus americana* is present will the vegetation grow higher. In a few such boggy areas the base of the trunk of trees of *Fraxinus nigra* is greatly enlarged (Gates & Erlanson 1925). As the association is rarely very dense, the conditions near the ground are favorable to a large number of secondary species. Many of the secondary species merely occur on wet ground, while others are characteristic of bogs and still others of upland associations. Such areas are very favorable to birds and insects as well as to tree seedlings. Only those of *Thuja occidentalis* are expected to result in succession, however, unless the area is being changed from a low area to upland. In the latter situation the maple-beech forest species more frequently invade and attain dominance. The lowland forest association will follow any herbaceous or shrub association on wet ground. Most frequently the associations which precede it are the Salix-Cornus thicket association and the Iris association.

There is normally at least slight drainage present where the lowland forest develops best, although drained conditions in wet areas by no means predicate the development of lowland forest.

The Fireweed Association

When low, wet or boggy areas are burned over the resulting conditions are exceptionally favorable to the development of the fireweed association. The

very large amount of organic matter, as well as the recently released mineral matter and the proximity to abundant water result in the germination of almost any seeds that get into the area. The soil reaction immediately after a fire is normally acid but this acid is leached nearly or quite out of the soil by the time plants are growing in it. The establishment of the association depends upon the time of year the area was burned, the proximity of seed plants, the dissemination of seeds into the area, and the longevity of those that survived the fire. In the case of early spring fires, the fireweed association may appear within a month. In summer fires, there may be a sprinkling of fireweeds that fall and an excellent association of them the following growing season, or sometimes there may be none until the following growing season. Vegetation does not follow fall fires until the next growing season. These are the results in areas that have been not too severely burned, that is not burned down to and into the humus of the soil. If the latter is the case, the seeds that are at or near the surface are destroyed, which necessitates a fresh distribution of seeds before vegetation can occupy the ground. In some cases it may then take two or even three years before revegetation occurs. The fireweed association is most widespread and best developed after the first severe fire in an area. Following subsequent fires in the course of which there has been less material to burn, there is poorer development of the fireweed association, indeed in many cases scarcely any development that properly may be called the fireweed association. Examples of this latter occur most frequently in areas occupied by the aspen association. Fires here are normally followed by vegetative multiplication from the aspen roots. The root suckers are usually so numerous that fireweeds, because of their intolerance to shade, cannot develop.

In spite of the lack of competition that might be expected to limit the duration of the fireweed association, an area is seldom thoroughly dominated by this association for more than one year. Even if no other plants invade the area in succeeding years, the fireweed cover is very much thinned out and bare ground may be noticed. This condition remains unless there should be a subsequent fire or until there is regeneration from stumps, where that is possible, or other plants invade and develop.

Of the different fireweeds that are present in this region, first place must be given to the fireweed *(Epilobium angustifolium)* which is exceedingly abundant. It occurs not only in the fireweed association, but also in limited quantities in almost all of the land associations. Its seeds are small, wind distributed and are borne in great abundance. They ripen from July until frost and may germinate immediately or lie over winter. The second fireweed in boggy areas is *Erigeron canadensis.* It is somewhat similar to Epilobium in general shape, but more bushy at the top and large plants may bear four or five times as many seeds. Another fireweed found in a few of the boggy areas is the sheep sorrel *(Rumex acetosella)* which is more characteristic of

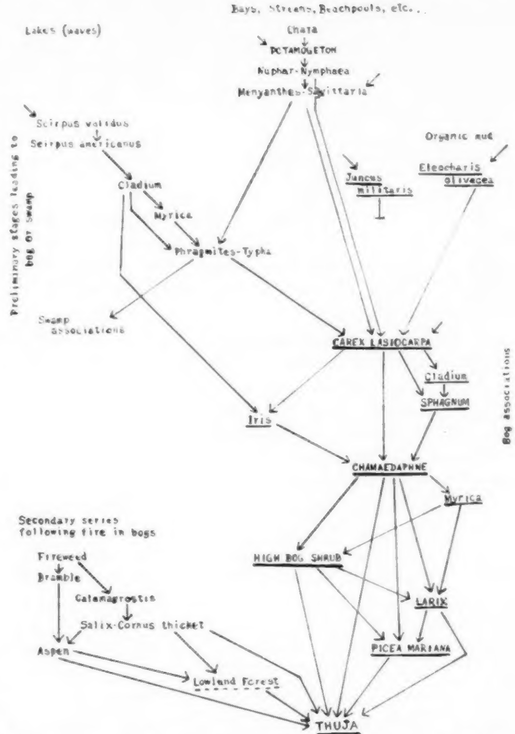


FIG. 32. Diagram showing successional relationships exhibited between the associations of bogs in northern Lower Michigan together with the associations in aquatic habitats leading to bogs and the principal successions following the burning of the vegetation in various bog habitats. The bog associations are underlined. The broken underline indicates that the Lowland forest may occur either in bog or swamp habitats. An arrowhead indicates the direction of succession; a cross line at end, that the succession usually terminates here; an arrow from the open means that the association may start *de novo;* and capital letters denote the most important associations.

sandy areas, but nevertheless Larix areas occasionally become covered with sheep sorrel after the Larix has been burned off. Many other plants, especially composites, or such grasses as *Agrostis scabra* (Fig. 28), may at times act as fireweeds in certain situations.

The association preceding the fireweed association is a matter of relatively no importance as the ground is opened up by any fire, whatever happens to be the material burned. Following the fireweed association on low ground, it is usual to have a bramble thicket or a thicket of other shrubs. Since the trees natural on boggy areas do not regenerate, seeding must take place, but conditions necessary for seeding and for seed development are so good that this has taken place quite rapidly in most of the burned-over boggy areas in the region, leading to the replacement of the Thuja association. If, however, the fire is repeated within a year or two, conditions are more favorable to the aspens, particularly *Populus tremu-*

loides. This development leads to a low aspen covered area which is permanently established if fires run through sufficiently often to burn up any seedlings of Thuja which might have become established. In such cases fires are of an advantage rather than otherwise to an aspen association, not only in eliminating the seedlings of trees which would grow higher, but also in increasing the density of the aspen grove, due to the fact that several sprouts come from one stump.

Bramble Association

The bramble association is an association of shrubby plants of the genus Rubus which occurs following fireweeds quite generally in areas that have not been too severely nor too frequently burned over. Brambles may appear as early as the second year, but it is more likely that three or four years will pass before they dominate. The seeds are distributed to the area by birds or sometimes by washing, especially in early spring when the ground is frozen. On boggy areas the bramble growth is not so well developed nor so extensive as on upland areas. Where brambles do occur, however, they are expected to be succeeded by the Thuja association unless fires again occur, in which case aspens are rather more likely to get a chance.

Aspen Association

Of the associations following fire, the aspen obtains greatest prominence because it is composed of trees which impress the eye to a greater degree and because it is so much longer lived than the other fire associations. While the aspen association covers all types of soils extensively (Gates 1930), the consideration here is limited to its appearance in boggy areas. The dominant trees under bog conditions are almost without exception *Populus tremuloides* which may make up almost 100 percent of the trees present in a well-developed lowland aspen area. Occasionally *Acer rubrum* or *Fraxinus nigra* may be present, but seldom in quantity unless succession is well under way. In boggy areas the importance of lack of shade is not quite so outstanding as in the upland areas since under bog conditions *Populus tremuloides* does stand slight shading. If the aspen association becomes reasonably established following the first burn, it will become thoroughly developed after two or three burns, following which it may remain for a long time, provided it is not succeeded or provided an occasional fire burns out seedlings that would otherwise replace it. In the bog habitat the life of aspen is longer than it is in other habitats and the trees may become considerably larger even as high as 20 m. with trunk diameters of up to and occasionally over 30 cm. The trees are usually rather weak and subject to breakage by wind, but in the bog habitat appear to be more thrifty than in upland habitats. As the stand is so dense in boggy areas, the shade cast greatly limits the number of plants that grow on the ground.

The association appears in the first place on areas which have been burned over and vegetated for a year or two with fireweeds. No cases have been noted where the aspen association started directly on the mineral soil although it seems most improbable that its seeds were not present there in view of the immense quantities produced by trees so widely distributed in this area. Suitable conditions for their start generally mean wet ground and damp air for a week or so to give the seeds a chance to germinate and become established. The natural water in the habitat of bogs greatly favors this establishment. The seedlings must then compete, but in the cases noted, the fireweeds were not extensively numerous and shrubs, most of which are bird distributed, are not present in great quantities as the area has not been sufficiently attractive to birds. The aspen grows but a few inches the first year, during which the mortality is highest. If it has not been killed by the end of the second year, it is likely to make a tree. The association thus developed is very spotted. To develop a uniform aspen cover requires either sufficient time for root suckers to come up in open places or more usually a combination of root suckers and stump sprouts following fires through the area, giving the other species a greater setback than that experienced by aspen itself.

The aspen association does not invade a tree or shrub covered bog area previous to burning. The Thuja association readily invades the aspen association on boggy ground and replaces it as soon as the Thuja trees begin to shade the aspen trees. In a few places in this region where the area is in the process of changing from a lowland to an upland area the Picea-Abies association is replacing the aspen.

In the following table (Table 5) the presence of a species in any association is indicated by the following letters: D = dominant species, d = subdominant, s = secondary species, i = invading species, and r = relic species. If any are included in parentheses ( ), it means that some setback has occurred, such as fire.

DENSITY OF VEGETATION

The density of the vegetation in various bog associations was taken by approximating the amount of coverage of each of the four fundamental layers or stories in each situation. The stories represented in the bogs here are the tree layer above 3 meters from the ground, a high shrub layer, mostly about 2 meters above ground, a low shrub layer, about a meter or a little less high, and the ground layer. With so many areas in the process of succession, a considerable amount of variation in the figures is to be expected; consequently, the range of values is given in Table 6. Inspection of the table brings out the easily observable fact that the ground is but sparsely covered in the pioneer association, *Carex lasiocarpa*. A nearly complete cover obtains in the Chamaedaphne association following, because of the growth of Sphagnum. Shade of the high bog shrub association is likewise greater than that of the Larix or Picea associations which often follow it. The climax bog

TABLE 5. Classified list of the more common or important species of plants of the bog associations of the Douglas Lake region.

Plants ↓ Associations →	Phase: Aquatic				Marsh						Shrub			Tree			Secondary			
	Potamogeton A.	Nuphar-Nymphaea A.	Eleocharis A.	Menyanthes-Sagittaria A.	Scirpus validus A.	Cladium A.	Sphagnum A.	Phragmites-Typha A.	CAREX LASIOCARPA A.	Iris A.	CHAMAEDAPHNE A.	Myrica A.	HIGH BOG SHRUB A.	Larix A.	Picea A.	THUJA A.	Fireweed A.	Salix-Cornus Thicket A.	Lowland Aspen A.	Lowland Forest A.
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
PLANTS SUBMERGED OR MOSTLY COVERED WITH WATER																				
Potamogeton pusillus L.	D																			
" *heterophyllus* Schreb.	D																			
Scirpus subterminalis Torr.	D																			
Lycopodium innundatum L.							s													
Utricularia intermedia Hayne		s					s													
" *vulgaris americana* A. Gray	s	s	s	r	r															
Sphagnum spp.							D		i											
WITH LEAVES FLOATING ON SURFACE OF WATER																				
Nuphar advena Ait.		D	r		r	r	r		r		r									
Nymphaea odorata Ait.		D			r		r		r											
Polygonum amphibium L.		D	r			r			r	r								r		
Potamogeton heterophyllus Schreb.		s	s		r			r	r	r										
" *natans* L.		D	r		r															
Sparganium minimum Fries.		i	D	r																
HERBACEOUS PLANTS WITH LEAVES PROJECTING ABOVE WATER OR WHOLLY IN THE AIR																				
Bryophytes:																				
Sphagnum spp.											s		s	s	s	r				
Pteridophytes: (sensu strictu)																				
Athyrium "filix-foemina"														s	s	s			r	
Botrychium virginianum (L.) Sw.														s	s	s			r	
Dryopteris thelypteris (L.) A. Gray										D	r		r	r				r	r	
Onoclea sensibilis L.													s	s	s	s		s	r	r
Osmunda cinnamomea L.											s		s	s	s			s	r	r
" *regalis* L.											s	s	s	s	s			s	r	r
Pteridium latiusculum (Pteris aquilina L.)																i			d	
Calamophytes:																				
Equisetum fluviatile L.					D															
" *scirpoides* Michx.																s				
" *sylvaticum* L.																s			r	r
Monocots: Cyperaceae (Sedges)																				
Carex bebbii Olney																s				
" *crinita* Lam.																s				
" *flava* L.												s								
" *gracillima* Schwein.															s	s			r	r
" *hystericina* Muhl.										s				s						
" *intumescens* Rudge																s			r	
" *lasiocarpa* Ehrh.		i	i	i	i	r?	r		D	r	r		r	r						
" *laxiflora* Lam.																			r	
" *lenticularis* Michx.												s								
" *leptalea* Wahlenb.														s	s	s			r	
" *limosa* L.										s	s									
" *oligosperma* Michx.						s			s											
" *pauciflora* Lightf.							s				s									
" *paupercula irrigua* (Wahlenb.) Fernald											s									
" *retrorsa* Schwein.																s				
" *rostrata* Stokes																s				
" *trisperma* Dewey															s	s				
several additional species are present in small numbers in wooded bogs.																				
Dulicheum arundinaceum (L.) Britton			s	i					s	s										
Eleocharis acuminata (Muhl.) Nees			D						r	r	r									

TABLE 5. *(Continued.)*

	PHASE																			
	AQUATIC				MARSH						SHRUB			TREE			SECONDARY			
Plants ↓ Associations →	Potamogeton A.	Nuphar-Nymphaea A.	Eleocharis A.	Menyanthes-Sagittaria A.	Scirpus validus A.	Cladium A.	Sphagnum A.	Phragmites-Typha A.	CAREX LASIOCARPA A.	Iris A.	CHAMAEDAPHNE A.	Myrica A.	HIGH BOG SHRUB A.	Larix A.	Picea A.	THUJA A.	Fireweed A.	Salix-Cornus Thicket A.	Lowland Aspen A.	Lowland Forest A.
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Monocots: Cyperaceae (Sedges) (Cont.)																				
Eleocharis olivacea Torr.		i	D																	
" *palustris* (L.) R. & S.								r	r	r										
" *tenuis* (Willd.) Schultes			D																	
Eriophorum callithrix Cham.											s									
" *virginicum* L.									i		s						d			
" *viridi-carinatum* (Engelm.) Fernald									i	s	s			r					r	
Mariscus mariscoides (Muhl.) Kuntze			i		i	D			r	r	r	r								
Rynchospora alba (L.) Vahl			s			s														
" *capillacea* Torr.			s																	
" *fusca* (L.) Ait. f.						s														
Scirpus atrocinctus Fernald									i		(i)		s	s			D	r	r	
" *atrovirens* Muhl.														s					r	r
" *cyperinus pelius* Fernald									(i)								s		r	r
" *hudsonicus* (Michx.) Fernald			s			s	s													
" *acutus* Muhl.		i			D			r	r		r							r		
" *validus* Vahl		i			D				r											
Juncaceae: (Rushes)																				
Juncus militaris Bigel. in *Juncus militaris* association.																				
Juncus pelocarpus Mey.						s														
Poaceae: (Grasses)																				
Bromus ciliatus L.														s						s
Calamagrostis canadensis (Michx.) Beauv.									i	i			r	r				r		
Cinna latifolia (Trev.) Griseb.														s						s
Glyceria borealis (Nash) Batchelder				s	s				s	s			s							
" *striata* (Lam.) Hitchc.			i							s			s	s				s	r	
Hierochloe odorata (L.) Wahlenb.												s								s
Leersia oryzoides (L.) Sw.			i						s											
Muhlenbergia mexicana (L.) Trin.													s							s
Phalaris arundinacea L.						s						r								
Phragmites communis Trin.		i			i			D										r		
Orchidaceae: (Orchids)																				
Arethusa bulbosa L.						s			s		s									
Calopogon pulchellus (Sw.) R. Br.											s									
Corallorrhiza trifida Chatelain																s				
Cypripedium parviflorum Salisb.														s		s				
" *reginae* Walt.														s		s				
Epipactis repens ophioides (Fernald) A. A. Eaton																s				
" *pubescens* (Willd.) A. A. Eaton																s				
Habenaria blephariglottis (Willd.) Torr.											s									
" *clavellata* (Michx.) Spreng.																s				
" *hyperborea* (L.) R. Br.													s	s	s	s				
" *leucophaea* (Nutt.) Gray									s											
" *obtusata* (Pursh.) Richards																s				
" *psychodes* (L.) Sw.												s								
Liparis loeselii (L.) Richard																s				
Listera convallarioides (Sw.) Torr.																s				
" *cordata* (L.) R. Br.																s				
Microstylis monophyllos (L.) Lindl.																s				
Pogonia ophioglossoides (L.) Ker.						s			s		s									
Spiranthes spp.											s									
Monocots not previously mentioned																				
Calla palustris L.																s				
Clintonia borealis (Ait.) Raf.														s	s	s				
Iris versicolor L.			i	i				i	i	D	r	r	r	r				r		r
Iris virginica L.			i						i	D	r		r	r						

TABLE 5. *(Continued.)*

Plants ↓ Associations →	Phase: Aquatic				Marsh						Shrub			Tree			Secondary			
	Potamogeton A.	Nuphar-Nymphaea A.	Eleocharis A.	Menyanthes-Sagittaria A.	Scirpus validus A.	Cladium A.	Sphagnum A.	Phragmites-Typha A.	CAREX LASIOCARPA A.	Iris A.	CHAMAEDAPHNE A.	Myrica A.	HIGH BOG SHRUB A.	Larix A.	Picea A.	THUJA A.	Fireweed A.	Salix-Cornus Thicket A.	Lowland Aspen A.	Lowland Forest A.
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Monocots not previously mentioned (Cont.)																				
Lilium philadelphicum andinum (Nutt.) Ker.															s	s				
Maianthemum canadense Desf.														r	r	r				
Sagittaria latifolia Willd.		i		D						r										
Scheuchzeria palustris L.									s		s									
Smilicina trifolia (L.) Desf.											s		s	s	s	s				
Sparganium diversifolium Graebner				s																
" *simplex* Huds.				s																
Streptopus amplexifolius (L.) DC.																s			r	
Triglochin maritima L.						s			s											
Trillium cernuum L.																s			r	
Typha latifolia L.					i			D	i	r	(i)		r	r				r		r
HERBS: DICOTYLEDONEAE-AXIFLORAE (AXIS FLOWER DICOTS)																				
Actaea rubra (Ait.) Willd.																s			r	
Anemone canadensis L.													s	s						
Asclepias incarnata L.					i					D								r		
Caltha palustris L.														s		s		r	r	
Coptis trifolia (L.) Salisb.														s	s	s			r	
Gentiana andrewsii Griseb.										s										
" *grayi* Kusnezow										s										
Halenia deflexa (Sm.) Griseb.																s				
Hypericum virginicum L.			i			i		s		D										
Hypopitys lanuginosa Nutt.																s			r	
Impatiens biflora Walt.																		s	r	
Lappula virginiana (L.) Greene																				s
Lychnis alba Mill.																	D			
Lycopus americanus Muhl.										D	r		r	r		r			r	
" *uniflorus* Michx.																		s	r	
Lysimachia terrestris (L.) BSP.										D	r	r		r			D	r	r	
Menyanthes trifoliata L.		i		D	r	r	r	r	r	r	r									
Moneses uniflora (L.) Gray																s				
Polygala pauciflora Willd.														s	s	s		r	r	
Polygonum punctatum Ell.																		s	s	s
Prunella vulgaris L.														s		s		s	r	
Pyrola asarifolia Michx.														s		s				
" *secunda* L.														s	s	s			s	
" *uliginosa* Torr.																s				
Ranunculus abortivus L.													s						r	s
" *pennsylvanicus* L. f.													s	s		s		s		
" *recurvatus* Poir.																s			r	
" *sceleratus* L.			i														D			
" *septentrionalis* Poir.													s						r	s
Rumex acetosella L.														s			D		s	
Sarracenia purpurea L.											s									
Steironema ciliatum (L.) Raf.																				s
Thalictrum dasycarpum Fisch. & Lall.												s	s					s	r	r
Viola canadensis L.														s		s			r	
" *pallens* (Banks) Brainerd.											s		s	s	s	s			r	
" *papilionacea* Pursh.																		s	r	s
HERBS: DICOTYLEDONEAE-CALYCIFLORAE (CUP FLOWER DICOTS) Except composites.																				
Aralia nudicaulis L.														s	s	s			s	
" *racemosa* L.																s				s
Campanula aparinoides Pursh.										s		s						s		
Cicuta bulbifera L.				s						s										
" *maculata* L.								s		s								r		

TABLE 5. *(Continued.)*

Plants ↓ / Associations →	Aquatic: Potamogeton A.	Aquatic: Nuphar-Nymphaea A.	Aquatic: Eleocharis A.	Aquatic: Menyanthes-Sagittaria A.	Marsh: Scirpus validus A.	Marsh: Cladium A.	Marsh: Sphagnum A.	Marsh: Phragmites-Typha A.	Marsh: CAREX LASIOCARPA A.	Marsh: Iris A.	Shrub: CHAMAEDAPHNE A.	Shrub: Myrica A.	Shrub: HIGH BOG SHRUB A.	Tree: Larix A.	Tree: Picea A.	Tree: THUJA A.	Secondary: Fireweed A.	Secondary: Salix-Cornus Thicket A.	Secondary: Lowland Aspen A.	Secondary: Lowland Forest A.
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Herbs: Dicotyledoneae - Calyciflorae (Cont.)																				
Circaea alpina L.																s			r	
Drosera intermedia Hayne											s									
Drosera rotundifolia L.										s	s			s		s				
Epilobium adenocaulon Haussk.										s	s						D	r		
" *angustifolium* L.														r		r	D	r		
Fragaria virginiana Duchesne														s	s	s		s	s	s
Galium boreale L.												s								
" *trifidum* L.									s	s				s		s		s	s	
" *triflorum* Michx.														s	s	s			r	s
Geum canadense Jacq.																				s
" *macrophyllum* Willd.														s						s
" *rivale* L.														s				s	r	
" *strictum* Ait.														s					r	s
Lobelia cardinalis L.										s			r					r		
Mitella nuda L.														s	s	s			r	
Potentilla canadensis L.														s						
" *palustris* (L.) Scop.				s		s		s	s	r	r									
Proserpinaca palustris L.				s																
Sanicula gregaria Bicknell																s				
HERBS: COMPOSITAE																				
Aster junceus Ait.						i		i	i	D	r			r					r	
" *lateriflorus* (L.) Britton														s	s	s				s
" *novae-angliae* L.														s	s	s			s	s
" *tradescanti* L.																			r	
" *salicifolius* Ait.																			s	
Bidens cernua L.			s																	
" *vulgata* Greene										s							D			
Cirsium muticum Michx.										s			s	s		r		s		r
Erigeron canadensis L.																	D		r	
" *philadelphicus* L.														s						s
" *ramosus* (Walt.) BSP														s				s		s
Eupatorium perfoliatum L.					i					D			r	r	r	r		r	r	r
" *purpureum* L.					i					D			r	r	r	r		r	r	r
" *purpureum maculatum* (L.) Darl.										D			r	r				r		
Gnaphalium uliginosum L.																s				s
Hieracium aurantiacum L.																			s	
Lactuca canadensis L.													s	s			D		s	s
Petasites palmata (Ait.) A. Gray																s				
Senecio balsamitae Muhl.																			s	
Solidago canadensis L.																	D		s	s
" *graminifolia* (L.) Salisb.								i	i	D		r					s	s	s	
" *rugosa* Mill.														s	s	s		s	r	
" *uliginosa* Nutt.														s	s	s				
LOW OR PROSTRATE DICOTYLEDONOUS SHRUBS (CHAMAEPHYTES)																				
Chiogenes hispidula (L.) T. & G.														s	s	s				
Cornus canadensis L.														s	s	s			r	
Gaultheria procumbens L.																(s)				
Linnaea borealis americana (Forbes) Rehder.														s	s	s			r	
Rubus triflorus Richards										s			s	s	s	s			r	
Vaccinium oxycoccus L.											D			r	r	r				
" *macrocarpon* Ait.											D									
MEDIUM HIGH SHRUBS (HIGH CHAMAEPHYTES) NANOPHANEROPHYTES																				
Andromeda glaucophylla Link									i		D		r	r	r	r				
Chamaedaphne calyculata (L.) Moench.		i		i					i	i	D		r	r	r	r		r	r	

TABLE 5. *(Continued.)*

Plants ↓ / Associations →	Phase																			
	Aquatic				Marsh						Shrub			Tree			Secondary			
	Potamogeton A.	Nuphar-Nymphaea A.	Eleocharis A.	Menyanthes-Sagittaria A.	Scirpus validus A.	Cladium A.	Sphagnum A.	Phragmites-Typha A.	CAREX LASIOCARPA A.	Iris A.	CHAMAEDAPHNE A.	Myrica A.	HIGH BOG SHRUB A.	Larix A.	Picea A.	THUJA A.	Fireweed A.	Salix-Cornus Thicket A.	Lowland Aspen A.	Lowland Forest A.
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Medium high shrubs (Cont.)																				
Diervilla lonicera Mill.																r			d	
Kalmia polifolia Wang.											D			r	r	r				
Ledum groenlandicum Oeder											D			r	r	r				
Lonicera canadensis Marsh.														s					s	
" *dioica* L.														s		s			s	
" *oblongifolia* (Goldie) Hook.													s	s	s					
Myrica gale L.						i			i	i	i	D	r	r	r					
Rhamnus alnifolia L'Her												D	r	r						
Rhus toxicodendron L.														s		s			s	
Ribes cynosbati L.														s		s		r		
" *hudsonianum* Richards																s				
" *glandulosum* Grauer																s				
" *triste* Pall.														s		s				
Salix candida Fluegge									i		i	D								
Taxus canadensis Marsh.																s				
Vaccinium canadense Kalm.											s			r	r	r			r	
" *pennsylvanicum* Lam.											s			r	r	r			r	
HIGH SHRUBS (HIGH NANOPHANEROPHYTES) MICROPHANEROPHYTES																				
Acer spicatum Lam.														s		s			i	s
Alnus incana (L.) Moench									i	i	i	i	D	r		r		i	i	r
Amelanchier spicata (Lam.) C. Koch.														s					s	
Aronia arbutifolia (L.) Ell.										i	i		D	r	r	r		i		
" *atropurpurea* Britton											i		D							
" *melanocarpa* (Michx.) Britton														r		r				
Betula glandulifera Butter									i		i	i	D	r	r					
Cornus alternifolia L. f.														s					s	s
" *rugosa* Lam.														s					s	
" *stolonifera* Michx.								i	i	i	i	i	r	r	r	r		D		
Ilex verticillata (L.) Gray											i	i	D	r	r	r		i		
Lonicera glaucescens Rydb.																s				
" *hirsuta* Eat.																s				
Nemopanthus mucronata (L.) Trel.											i	i	D	r	r	r			r	
Physocarpus opulifolius (L.) Maxim.													s							
Rosa schuetteana E. W. Erlanson										i		i		r				D		
Rubus alleghiensis Porter														r						
" *strigosus* Michx.														r					r	r
Spiraea alba DuRoi									i		i		s	r				D		
Salix bebbiana Sarg.										i				r	r	r	i	D	s	r
" *discolor* Muhl.										i				r	r	r	i	D	s	r
" *lucida* Muhl.									i	i	i	i	r	r	r	r	i	D	s	r
" *pedicellaris* Pursh.									i		i		D	r						
" *serissima* (Bailey) Fernald													D	r				D		
Viburnum cassinoides L.													D	r	r	r		D		
" *opulus* L. var.													D					D		
VINE																				
Clematis virginiana L.														s				s		
LIANAS																				
Celastrus scandens L.																		s		
Parthenocissus quinquefolia (L.) Planch.													s					s		
Vitus vulpina L.																		s		
ANGIOSPERMOUS PARASITE																				
Arceuthobium pusillum Peck															s					
TREES-DECIDUOUS, MESOPHANEROPHYTES																				
Acer rubrum L.									i	i	i		i	s		r		i	s	D
" *saccharum* Marsh.																i			i	i

TABLE 5. *(Continued.)*

Plants ↓ / Associations →	PHASE: AQUATIC				MARSH						SHRUB			TREE			SECONDARY			
	Potamogeton A.	Nuphar-Nymphaea A.	Eleocharis A.	Menyanthes-Sagittaria A.	Scirpus validus A.	Cladium A.	Sphagnum A.	Phragmites-Typha A.	CAREX LASIOCARPA A.	Iris A.	CHAMAEDAPHNE A.	Myrica A.	HIGH BOG SHRUB A.	Larix A.	Picea A.	THUJA A.	Fireweed A.	Salix-Cornus Thicket A.	Lowland Aspen A.	Lowland Forest A.
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Trees - deciduous, Mesophanerophytes (Cont.)																				
Betula lutea Michx. f.																i			i	i
" *papyrifera* Marsh.											i	i		r	r	r	i		D	
Fagus grandifolia Ehrh.																i			i	
Fraxinus nigra Marsh.										i		i	i	s		r		i	i	D
Larix laricina (DuRoi) Koch.											i			D	r	r	i	i		
Populus balsamifera L.												i		r		r			s	
" *tremuloides* Michx.											i	i		r	r	r	i	i	D	r
Prunus pennsylvanica L. f.														r		r				
Quercus borealis Michx. f.											i			i		i				
Sorbus americana Marsh.														s		s				
Ulmus americana L.										i			i	i		r		i	i	D
TREES - EVERGREEN, MESOPHANEROPHYTES																				
Abies balsamea (L.) Mill.														i	s	s			i	i
Picea glauca Voss. (P. canadensis)													i	i	i	s			i	i
" *mariana* (Mill.) BSP											i		i	i	D	r			i	
Pinus strobus L.											i				i	i			i	
Thuja occidentalis L.										i	i	i	i	i	i	D		i	i	i

association, the Thuja, casts nearly complete shade and it is only in open places where trees have fallen that ground plants have a chance to develop.

TABLE 6. Density of vegetation in the important bog associations expressed as percentages of complete coverage (100 percent) at various levels, each level considered by itself. (The figures give the range of values usually found.)

Levels	*Carex lasiocarpa*	Chamaedaphne	High bog shrub	Larix	Picea	Thuja
Tree level	0	0-0.1	0-1±	25-40	40-50	50-85
High shrub level	0	0-2	20-75	20-30	10-15	1-3
Low shrub level, mostly Chamaedaphne	0	35-90	20-55	1-20	1-15±	1-4
Ground level, made up of:	2-5	10-95	5-20	35-70	8-80±	0.2-15±
Woody species invading	(0-0.1)	(1-10±)	(2-5)	(10-40)	(2-10)	(0-0.1)
Sedges (+the few grasses)	(1-5)	(1-6)	(0.5-3.5)	(0.5-8)	(0.5-5)	(0.5-2)
Forbs	(0-0.2)	(1-3)	(0.1-1)	(18-35)	(4-6)	(0.5-4)
Mosses (including Sphagnums)	(0-0.1)	(40-95)	(0-10)	(1-45)	(4-65)	(1-15)

VEGETATION FORMULAS

Although vegetation formulas for the various associations would make it possible to interpret the different associations mathematically, no really satisfactory formula has ever been devised. An approach in that direction put forward by L. Dudley Stamp (1929) has been here modified slightly to serve as a basis for Table 7, which contains vegetation formulas for the various associations in different places in the region. In them exact details are so variable in the different places because of successional and other influences, that in Table 7 effort has been made to strike a medium which will permit an expression of developmental trends taking place during the course of succession. The formula is based on dividing the plants in vegetation into five categories: trees, shrubs, herbs, grasses or grasslike plants, and cryptogams, with secondary divisions where necessary. Trees are here divided into mature trees and seedlings and young saplings of invading tree species. The high and low shrubs are separated and the cryptogams are divided into ferns and moss cover. In each case the calculations express the number of individuals present in one square kilometer (hectar) of ground. With the mosses, individuals were not counted but the amount of coverage was measured and is expressed as proportion of full coverage, 1.0 being full

TABLE 7. Vegetation formulas for various associations studied.

	A (Trees) Tree and tree seedlings		F (Shrubs) High shrubs	F (Shrubs) Low shrubs	H (Herbs) Herbs	G (Grasses and grasslike plants) Sedges, grasses, rushes	C (Cryptogams) Ferns	Moss cover, 1 = full coverage
Carex lasiocarpa	O A		+ O F		+ 17,500 H	+ 3,500,000 G$\underline{a}$	+ O C	
Chamaedaphne	O A		+ O F	+ 1,500,000 F'$\underline{b}$	+ 25,000 Hx	+ 14,000 G	+ 250 C	+ C' 0.75
High bog shrub	O A	+ 22,000 A''	+ 140,000 F$\underline{c}$,x	+ 130,000 F'$\underline{b}$,x	+ 75,000 Hx	+ 184,000 G	+ 57,000 C	+ C' 0.01–0.4
Larix	7,000 A$\underline{d}$	+ 1,300 A''	+ 69,000 Fx	+ 250,000 F'x	+ 400,000 Hx	+ 450,000 G	+ 30,000 C	+ C' 0.2–0.5
Picea	23,000 A$\underline{e}$	+ 500 A''	+ 23,500 Fx	+ 851,000 F'x	+ 107,000 Hx	+ 1,000,000 G	+ 1,100 C	+ C' 0.75
Thuja	33,000 A$\underline{f}$	+ 100 A''	+ 20,000 Fx	+ 32,300 F'x	+ 218,000 Hx	+ 90,400 G	+ 500 C	+ C' 0.01–0.3

$\underline{a}$ = *Carex lasiocarpa* (underlining of letter indicates dominant species); $\underline{b}$ = *Chamaedaphne calyculata*; $\underline{c}$ = *Nemopanthus mucronatus*; $\underline{d}$ = *Larix laricina* (deciduous conifer); $\underline{e}$ = *Picea mariana* (evergreen conifer); $\underline{f}$ = *Thuja occidentalis* (evergreen conifer); x = others important; ' = subdivisions; '' = seedlings of invading species.

coverage. In this table no effort has been made to call attention to important species other than the dominant species in any of the associations. Addition of these figures gives an idea of the number of individual plants per hectar in the various associations, namely: *Carex lasiocarpa,* 3,517,500; Chamaedaphne, 1,539,250; high bog shrub, 608,000; Larix, 1,207,300; Picea, 2,006,100; and Thuja, 394,300.

As might be expected, regular progressions or retrogressions of the numbers are not always evident. The obvious explanation, especially in the case of the grasses and grasslike plants is the change from a few coarse to many fine species above the shrub associations. The Carex and Chamaedaphne associations may often be found without invading species but that is not the case with any of the other shrub or of the tree associations. Even in the Thuja association which terminates the bog series, invading species of the maple-beech association and occasionally of the pine association are present in numbers sufficient to be included in the table. Such invading species very seldom develop beyond the seedling stage under present conditions. Undoubtedly the time will come when succession will follow such invasions.

PEAT

In this region from which the Late Wisconsin glaciation has so recently retreated, the peat which has formed is nearly all in a semifluid or gelatinous condition in the depressions. No economic use has been made of it even in those few shallow places where it has become somewhat dried out. The accumulation of pollen grains in such semifluid peat does not permit accurate dating of the accumulations of peat in the region. The pollen work, which has been done on parts of bogs where the peat is less liquid than is most of the peat (Potzger 1932 and T. J. Cobbe, unpublished ms.), indicates that during the beginning of bog formation in the region, the vegetation was prevailingly coniferous, but in recent times the surroundings have changed from conifers to maple-beech and this is reflected in the ascendency of hardwood pollen in the upper 7.5 to 9 feet. Figures obtained by Sears in Ohio indicate that there it requires 300 years to make a foot of peat. That is obviously much too long for the conditions in this northern region, but no accurate figures are obtainable. The oldest trees of the maple-beech association in the region are now 390 years of age. Were it not for the lumberman, trees of this age would cover most of the upland of these two counties. Only two trees in the whole region have been found to be older. Both were trees of *Tsuga canadensis* which, were they alive at the present time, would be 520 and 540 years of age. Since the change from dominantly conifer pollen to dominantly hardwood pollen in the bogs studied took place rather suddenly, it would seem that the conifers of the areas surrounding the bogs were replaced *en masse*.

ECONOMICS

Although drained bogs often provide valuable land for agriculture, most of the bogs in the Douglas Lake region are too close to the water table to permit drainage. Furthermore, the agricultural value of what drained bogland there is, or of what might be obtained, in this northern area would doubtfully be equal to the value of the wooded bog as a water reservoir. Such a reservoir maintains a good water level in surrounding sandy land and a consistently satisfactory stream level for the production of fish. Wooded bogs also act as a valuable reservoir for wild life.

SUMMARY

1. This paper is based on work carried on during the past thirty years in the Douglas Lake region, which is located in the northern part of the overlapping zone between the northeastern coniferous forest province and the central deciduous forest province in the extreme northern part of the Lower Peninsula of Michigan.

2. The retreat of the Late Wisconsin glaciation left many places suitable for the development of bogs. Approximately one-third of the area is bogland in various stages of development or redevelopment following disturbance, or aquatic areas which may become bogs depending upon the vegetation that becomes established. All the bogs of the region are of the lowland type.

3. Outstanding characteristics of bogs include little or no drainage, poor aeration, little or no oxygen, low nitrogen content, low temperatures below the surface, in general cool climate, alkaline or acid water, a false bottom of organic mud or marly mud, a floating mat with acid reaction, and a marginal fosse. Wave action is normally absent or minor, likewise wind action except for violent storms, but ice action is often quite obvious.

4. The entrance of the mat-forming sedge, *Carex lasiocarpa*, is the most certain indication of the possible development of an aquatic area in the direction of a bog. By the activity of bog vegetation, open water is changed to land.

5. The most common typical sere in the bogs of the region is from aquatic associations or open water to the *Carex lasiocarpa* association, followed by the Chamaedaphne association, next the high bog shrub association in various manifestations, next tree associations, Larix and Picea and climaxed by the Thuja association. Succession beyond the bog is evident in a few places in the region.

6. The flora of bog associations becomes more numerous and diverse as marsh types of associations are succeeded by tree types.

7. Higher plant families well represented in bogs include: Ericaceae, Cyperaceae, Orchidaceae and Ranunculaceae. The number of monocotyledonous species is proportionally higher in bogs than in uplands, although the number of grasses is very small. Legumes are absent from the native bog flora.

8. With the increase of human interest in bogs, the flora has steadily diminished by the loss of showy species as well as rare ones.

9. Fires in bogs are favorable to the extension of the Chamaedaphne association at the expense of other associations.

10. Although bogs reclaimed by drainage are suitable as agricultural land, in this region bogs are more valuable as water reservoirs and both shelter and feeding ground for wildlife.

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VEGETATION OF THE NORTHERN PART OF CHERRY COUNTY, NEBRASKA*

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INTRODUCTION

Agricultural practices in the Great Plains of North America are now in a period of adjustment from a traditional agriculture initiated by pioneer farmers to a grazing economy based upon potentialities of climate and soil. The attainment of a proper system of land use has been retarded in many localities by the lack of definite information concerning the vegetation and its indicator significance. In this study of the vegetation of Cherry County, Nebraska, the interrelations between the plants and their environments are discussed, the dominant species are described, and changes in grasslands caused by seasons, grazing, and climatic cycles are explained.

Cherry County, which is located in north-central Nebraska, extends from 100°10′ to 102°2′ west longitude and from 42°7′ to 43° north latitude, distances of 96 and 63 miles, respectively. It is the largest county in Nebraska and includes an area of 6,048 square miles. More than 90 percent of this area lies in the sand-hill region. The remainder (the hardlands) consists of fine sandy loam soils, the main body of which is north of the Niobrara River and northeast of Minnechaduza Creek.

A study of the vegetation of the sand hills of Nebraska was first made by Pool (1914). Reviews of pioneer work on the taxonomy of various species may be found in his paper. Since then few studies have been made. Weaver (1920) described root systems of certain sand-hill plants, and Keim and Frolik (1932) studied the introduction of exotic legumes and grasses into wet meadows and recorded the effects upon productivity. Ramaley (1939) made a study of the flora of the sand hills of northeastern Colorado and compared it with the sand-hill flora of Nebraska.

According to information obtained from pioneers who are yet living, the dunes were not as well vegetated in the early years of settlement as they are at present. Blowouts were more common, and pioneer vegetation was more prevalent. An early resident stated that sand-hill bluestem (*Andropogon hallii* Hack.) was much more common than it is today. Little bluestem (*Andropogon scoparius* Michx.) was once dominant and led Pool (1913) to describe a "bunch-grass association." Early pictures verify Pool's conclusions (Anderson & Walker 1920) and also indicate that blowout grass (*Redfieldia flexuosa* (Thurb.) Vasey) and weedy plants like soapweed (*Yucca glauca* Nutt.) were once very common.

Changes in vegetation of the sand hills since their settlement by white men have accompanied the control of fires, and differences in land use and intensity of grazing. Before the development of ranching, prairie fires occurred throughout the region at varying intervals. These fires spread rapidly and generated intense heat wherever sufficient debris had accumulated. Buds were killed, even in the centers of the bunches of grass, and roots were burned. Severe wind erosion followed denudation, and most dunes were permanently capped with a blowout. After each fire pioneer grasses and forbs began a new succession of plants. Only after several years was enough litter again accumulated to feed new fires. Since the beginning of the present century grazing has checked this accumulation, and therefore fires have been under control. Dunes are now held in place and large blowouts are rare. Variation in composition of vegetation is now caused by grazing and local environments.

Areas of vegetation on government preserves or on private ranges which have been protected from both fire and grazing for many years indicate the potentialities of development of vegetation in the several environments. Modifications of composition regularly accompany shifts from one phase of the climatic cycle to another. The decrease of little bluestem during the recent dry years is a striking example.

The writer wishes to acknowledge his indebtedness to Dr. J. E. Weaver, professor of plant ecology at the University of Nebraska, for helpful suggestions and criticisms not only during the progress of this study but also in the presentation of the results. He is also indebted to the Nebraska Conservation and Survey Division, under the direction of Dr. G. E. Condra, for making possible the field studies upon which this report is based. Thanks are extended to Dr. Ward M. Sharp and Mr. Geno Amundsen, both of the United States Biological Survey, for assistance in numerous ways.

GEOLOGY AND SOILS

The controlling factors in development of drainage, topography, and soil lie in the stratigraphy, structure, and texture of the rocks. Sands and limy sandstones were deposited in two formations during Pleiocene times upon the Brule clay of Oligocene age. The Valentine sand formation was deposited to a depth of 75 feet directly above the Brule clay, and this was later capped with a limy sandstone which is called the Ash Hollow formation.

The parent materials of fine sandy loam soils are derived from the Ash Hollow formation. The chief area of such soils is located on the Crookston Table north of the Niobrara River in the northeastern corner of Cherry County. During the Pleistocene and recent times, runoff from these uplands has formed a water-erosion topography of ravines and deep canyons between relatively level tablelands. Water enters readily into dune sands which are located

south of the Niobrara River, and thus there is little runoff from the surface of the dunes. Here wind erosion has played a dominant role in the formation of a rough, irregular dune topography (Fig. 1).

FIG. 1. General view of sand-dune topography; the east end of Dewey Lake is in the background.

Water has eroded valleys and canyons into the sand hills only where its movement attains sufficient velocity and volume to carry a load of sand. The Niobrara River has cut across the sand hills in northern Cherry County and eroded through the Ash Hollow limy sandstone to points below the top of the Brule clay from Valentine eastward (Fig. 2). Tributaries of the Niobrara River also have eroded canyons and established surface drainage southward toward the interior of the sand hills, but drainage is yet immature in many areas. This results in a high water table which forms lakes in depressions and many acres of grassland are subirrigated in the broad, shallow valleys. Sand hills immediately adjacent to the deep canyons, however, are well drained and have a water table far beneath the surface. A system of lateral tributaries has not developed on either side of the permanent creeks and streams.

FIG. 2. General view of Niobrara Valley looking eastward from Fort Niobrara Game Preserve. Deciduous trees grow along the river and on the north slopes. Ponderosa pine is scattered over the mixed prairie grasslands on the south slopes and along the limy sandstone outcrops in the immediate right foreground. A good stand of western needlegrass occurs in the foreground.

Rain filters directly into dune sands with little or no surface runoff and reaches the water table except as removed by evaporation from the surface of the sand and by absorption and transpiration. The amount of rain that reaches the water table is therefore considerable, especially during years of heavy snow and early spring rain. After the development of vegetation begins in spring, rain seldoms falls in amounts sufficient for water to penetrate beyond the reach of the roots of plants. Sufficient water filters through the soils in ravines and along slopes of the canyons, however, to maintain a water table deep beneath the surface.

Streams and lakes in the sand hills constantly receive drainage from the ground water. The streams therefore have a continuous flow throughout the year, and seasonal fluctuations never exceed a few inches. In contrast, the creeks and rivers which receive surface drainage from hardlands are flooded by runoff water during heavy showers.

The Valentine Lakes receive water from springs concentrated along the south and west shores. Poorly drained lakes fluctuate in depth between periods of high rainfall and drought. Lakes with good surface drainage and an abundant supply of spring water do not have marked periodical fluctuations of the water level. Surface drainage prevents an accumulation of large quantities of water during periods of abundant rainfall, and a good supply of water from springs prevents excessive lowering of the level of the lake during drought.

Numerous small springs and seepages occur on the south side of the Niobrara Valley at a point of contact between the impervious Brule clay below and the sandy formations above. These are at the same level as the river near Valentine, but as the river erodes into the Brule clay they occur as much as 125 feet above the valley floor 15 to 20 miles east of Fort Niobrara Game Preserve. Only a small amount of moisture penetrates beyond the depth of plant roots in the fine sandy loam soils of the Crookston Table, and thus only a small quantity of moisture reaches the water table. Seepages have developed north of the Niobrara Valley only near the heads of the major canyons.

The lowest recorded elevation in Cherry County is 2,373 feet above sea level. The rise in elevation from the Niobrara Valley near Valentine southward to 3,001 feet near Kennedy is about 12 feet per mile. Nights are cool throughout the summer because of these elevations.

Little soil formation has taken place in the sandhill region because of wind erosion. The tops of the dunes have a coarser texture than the sides and adjacent dry meadows due to the selective action of wind erosion. Dune sands have little or no organic matter, but the dry meadows have been stable long enough for the accumulation of small quantities of

humus in the surface few inches. The latter are classified under the Valentine soil series.

In the surface sands in many wet meadows considerable organic matter has accumulated, and deposits of peat are found in old lake beds. Sands of the second and third foot levels have been modified by poor aeration and drainage. These are included under the Gannet soil series. They occur only in meadows adjacent to well drained lakes where the water table does not fluctuate more than 2 to 3 feet. A growth of mesophytic tall grasses occurs in this habitat.

Shores of lakes without surface drainage are subject to great fluctuations in the water table. Vegetation remains permanently in phases of development, and little humus accumulates in the sands.

Salts have accumulated in certain poorly drained wet meadows in sufficient quantity to inhibit all plant growth or all except that of the most salt-tolerant species.

Parent materials on the hardlands areas have undergone varying degrees of development, resulting in dark brown and Chernozem soils. Soils with deep, well developed profiles are found on the flats. These are included in the Holt series. Soils with shallow profiles occur on the low, rolling hills and are classified in the Rosebud series. Soils of considerable variation in texture occur on well drained terraces and hillsides. Mixed prairie grasses grow on the hardlands.

METHODS

Two centers of study were established in eastern Cherry County, one at the Valentine Lakes Refuge, and the other at Fort Niobrara Game Preserve. The former is a typical sand-hill area with poorly drained valleys. Grazing has been discontinued only since 1935, and much of the vegetation is disclimax. Both hardland and well drained sandy habitats are included in the Fort Niobrara Game Preserve. Much of this area has been protected since 1914, and vegetation is near maximum development. Stations were established in all typical types of vegetation in both areas. Work was concentrated at Dewey Lake in the Valentine Lakes Refuge in 1937 and at the Fort Niobrara Game Preserve in 1938.

Environmental data were obtained in prairie and woodland in 1936; in a wet meadow, a dry meadow, and on the south slope of a dune in 1937 and in a dry meadow, a mixed-prairie area, and on both a north and south slope of a dune in 1938. Precipitation records were those of the weather stations at Valentine and the Valentine Lakes Refuge. Measurements of soil moisture to a depth of 5 feet were made at weekly intervals at the various stations during the growing season of 1937 and 1938. Hygroscopic coefficients were obtained from representative samples from the surface 6 inches of soil, except in the wet meadow where samples were taken also at depths of 12 and 24 inches. Percentage of moisture above the hygroscopic coefficient was considered available to plant growth.

Soil and air temperatures at a depth of 3 inches and at a height of 4 inches, respectively, were recorded by thermographs. Relative humidity was measured by hygrographs and evaporation by Livingston's white spherical atmometers, each fitted with a nonabsorbing device. The atmometers were operated in pairs at a height of 3 inches above the soil surface. Readings were made each week and reduced to those of standard atmometers. Anemometers located 6 inches above the surface of the soil recorded wind movement in miles per week. Stakes were driven on the eroding side of a young blowout in the fall of 1937 to ascertain the rate of removal of sand by wind during the winter. Water level was measured by inserting one-inch iron pipes with sandpoints attached, to depths of 4 to 8 feet into the sand. Depth of water level was determined by inserting a weighted tape marked with chalk, which was readily wetted.

The boundaries of the communities included in this study were determined by ocular survey; roots were excavated; diagrams of both aerial and underground parts were made; and several hundred basal area and census quadrats were located at random within the several communities. Basal area was recorded in square centimeters. Bunches or stems of plants were used as units in listing, according to convenience.

ENVIRONMENT

The summer climate of this semiarid region is characterized by a growing season of moderate length, with occasional thundershowers, high daily temperatures, relatively cool nights, low relative humidities, high rates of evaporation, and prevailing south winds. The average frost-free period is 151 days.

The winters are moderately cold, with minimum temperatures as low as —10° to —38° F. Snowfall is light and of little value in restoration of moisture on the tablelands and windswept tops of sand dunes. Much of the snow is blown into low protected places or onto the leeward steep hillsides along the edges of the tablelands. Prevailing winds in winter are from the west and northwest.

PRECIPITATION AND SOIL MOISTURE

The average annual precipitation at Valentine for a period of 51 years, prior to 1938, was 18.3 inches. That during the growing season, April to September inclusive, was 14.9 inches. The great variation in precipitation is illustrated by the average annual rainfall during each of the 4-year periods ending in 1926, 1930, and 1934. The amounts were 17.3, 22.8, and 14.9 inches, respectively. The 3-year period ending in 1937 had an average annual rainfall of 13.4 inches. The year 1929 had a total rainfall of 28.9 inches, and 1937, 11.5 inches.

Rainfall at Valentine in 1935, was 1.5 inches below normal. March and April had a total precipitation of 14.6 inches, which was 4.5 inches above normal. The last half of the year, however, was

unusually dry with a total precipitation of only 2.9 inches, 4.8 inches below normal. This drought period continued through the entire year of 1936 with a total rainfall of only 12.5 inches or 5.9 inches below normal. It did not end until the fall of 1937 when 3.2 inches of rain fell late in August and early in September. Precipitation was plentiful in the spring of 1938 when 4.5 inches more than the normal amount fell from March to May, inclusive. Most of July was dry, but showers late in June and early in July prolonged the growing season. The late summer and entire fall were dry, with rainfall 3.5 inches below normal from June to October, inclusive.

Precipitation data for only 1937 and 1938 are available at the Valentine Lakes Refuge. Here the trend in rainfall was the same as that at Valentine. Both stations recorded 5.6 inches rain from July 1 to September 30, 1938, but at Valentine Lakes Refuge rains occurred in fewer and heavier showers, and were thus more efficient in replenishing soil moisture.

The quantity of available moisture is the most important single environmental factor in determining the composition of plant cover. The total quantity of moisture finally available in any upland environment is determined by the disposition of fallen moisture. This disposition is controlled by soil texture. Slight differences in the efficiency of absorption of rain as affected by soil texture is especially important in this semiarid region because small quantities of moisture determine the survival of vegetation in periods of drought.

The rate of infiltration is especially important because it determines the quantity of runoff. Even the heaviest rains are usually absorbed directly by dune sands, but considerable moisture is lost by runoff from fine sandy loams, especially during heavy thundershowers. The amount of water finally available further depends upon the quantity of moisture lost by evaporation from the surface and the amount lost by percolation deep into the sands beyond the zone of root growth.

Since the moisture holding capacity of sand is relatively low, rain penetrates deeper into sand than in hardland soils. Therefore less moisture is lost by evaporation from the surface of sand than from fine sandy loams.

Sand, which has a low moisture-holding capacity, loses considerable water by percolation beyond the zone of root growth, especially during winter and early spring. But this loss is unimportant because it occurs at a period of high rainfall and cool temperatures. Also vegetation is dormant during much of this period. Once growth and transpiration has passed the prevernal period, however, there is little loss to the water table. Since summer rains are absorbed with great efficiency, a considerable portion of rain falling in summer is available to plant roots in dune sand.

Fine textured soils have a higher moisture holding capacity than sand. Therefore considerable moisture is held in hardland soils from winter and early spring before transpiration from vegetation becomes great. But the absorption of rain falling in short, heavy showers is relatively inefficient because much water is lost by runoff and evaporation from the surface of the soil. The quantity of moisture available to plant roots from summer rain is small. Once the moisture stored during early spring is exhausted through transpiration, plants on the hardlands undergo long periods of summer drought.

Efficient absorption of rain during the critical months of summer is the controlling factor in distribution of the several kinds of upland dominant grasses of the region.

Data representing moisture content of sand on top of a dune are shown in Figure 3. The sampled areas were dominated by sand-hill muhley (***Muhlenbergia pungens*** Thurb.) and hairy grama (***Bouteloua hirsuta*** Lag.). Both in 1937 and 1938 available moisture persisted in the third to fifth foot throughout the growing season. Water in the surface 2 feet varied according to occurrence of showers, and the sand remained without available moisture at same level for 7 weeks during 1937, and for 6 consecutive weeks in the first foot in 1938.

The surface 6 inches in blowouts with no vegetation contained little moisture, except for periods immediately following rains, but the sands beneath the surface 6 inches were moist to approximately their field capacity. Moisture was also unavailable in the surface 6 inches of blowout sands with open stands of blowout grass, but the 0.5- to 3-foot level contained 1 to 2 percent available moisture on June 22, 1938, 22 days after the last shower.

Moisture in Valentine sand, with sand reedgrass (*Calamovilfa longifolia* (Hook.) Hack.) and sand dropseed (*Sporobolus cryptandrus* (Torr.) A. Gray), is recorded for 1937 and 1938 in Figure 4. These fine sands with hygroscopic coefficients approximating 2.5 percent did not absorb moisture as efficiently as sand on top of the dunes, but moisture holding capacity was higher. Available moisture was exhausted in the surface foot when samples were taken on July 17, 1936, and (except at two intervals) from June 15 to August 15 in 1937. As a result of good rains early in the summer of 1938, available water persisted in the surface foot until July 18, except during the third week of June. During 1937 available moisture in the 3- to 6-foot level was exhausted beginning the second week in June and in the second-foot level from the first week in July until late in August. Available water was then restored to the surface 3 feet as a result of 2.6 inches of rain. Soil moisture was depleted gradually in the summer of 1938, but persisted within the surface 5 feet until the last week in July; soon after this none was available until September 11.

Pioneer vegetation in blowouts and communities in early phases of development were slow to deplete moisture. It was available throughout the growing season at depths beyond 2 feet, but xerophytic grasses in well developed communities with large leaf and root surfaces readily absorbed available moisture

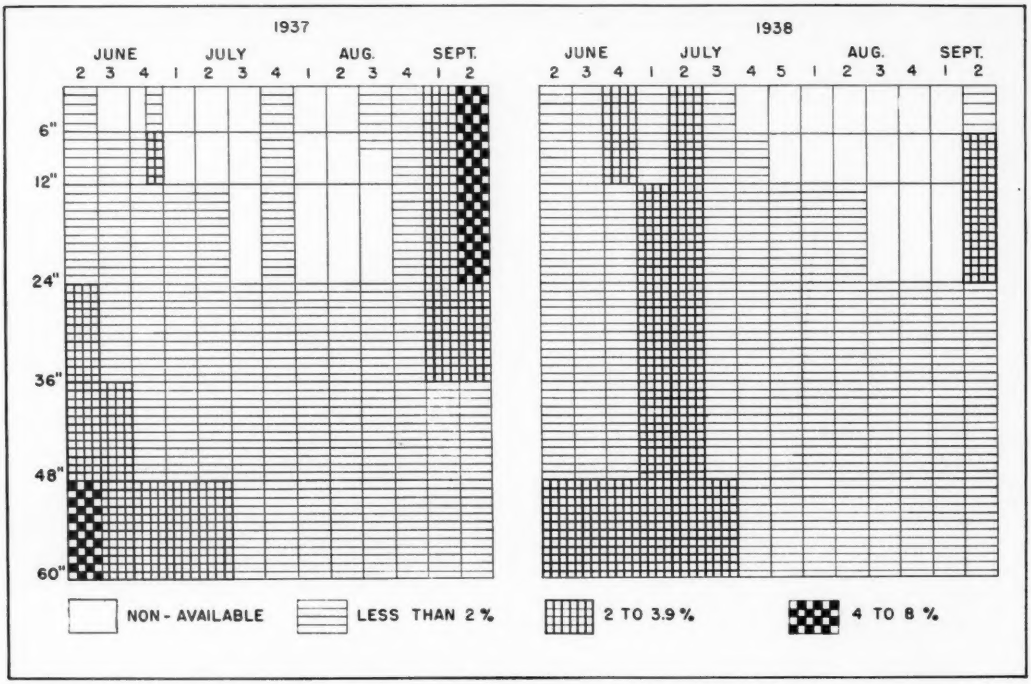

FIG. 3. Available water in the sand on top of a dune in the sand-hill muhley *(Muhlenbergia pungens)*—hairy grama *(Bouteloua gracilis)* community at Valentine Lakes Refuge during the summer of 1937 (left) and at Fort Niobrara Game Preserve (right) during the summer of 1938.

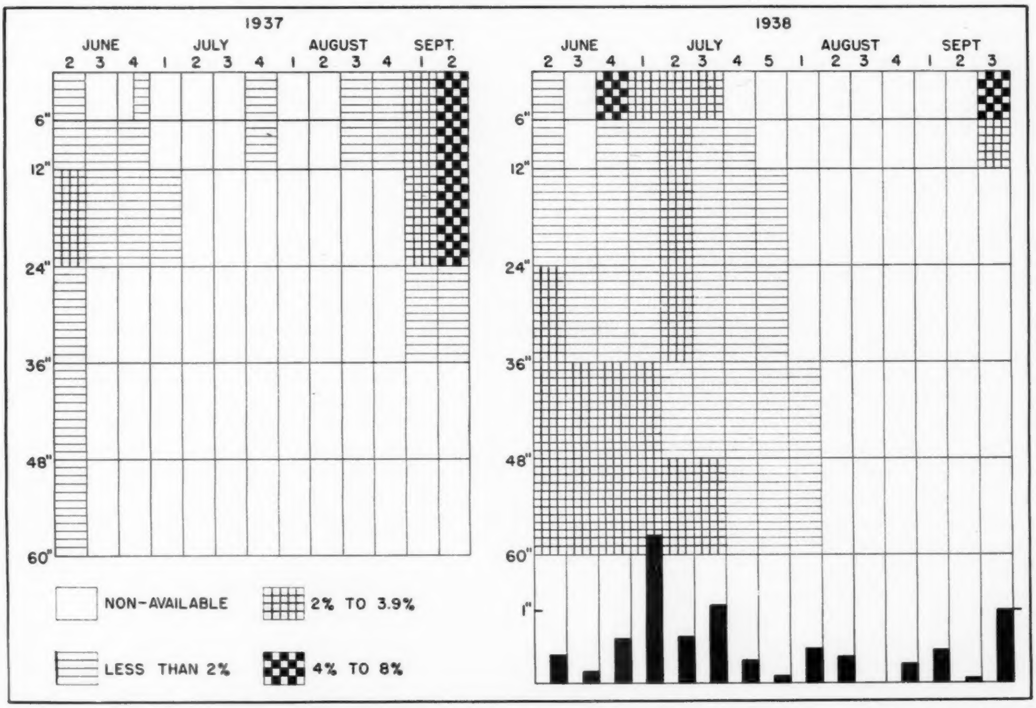

FIG. 4. Available water in Valentine sand in a dry meadow at Dewey Lake in the summer of 1937 (left) and at Fort Niobrara (right) in the summer of 1938. Weekly precipitation for 1938 is shown by vertical bars.

throughout the 4- to 5-foot soil levels and endured long periods of drought.

The efficiency of absorption of summer rain is materially reduced in fine sandy loam, but moisture holding capacity is high. Rainfall of early spring does not penetrate beyond reach of the grass roots, and water from small showers of only 0.2 to 0.4 inch does not penetrate deep enough to reach them. Only the heaviest summer rains are effective in restoring moisture. Available water in Rosebud fine sandy loam is shown in Figure 5. It was present to a depth of

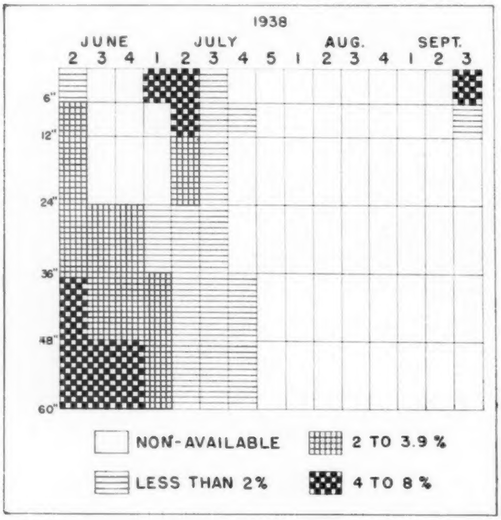

FIG. 5. Available moisture in soil in needlegrass *(Stipa comata)*-niggerwool *(Carex filifolia)* community on hardlands at Fort Niobrara Game Preserve during the summer of 1938.

4.5 feet by May 24, 1938. Soil moisture in this area, which was dominated by needle grass (*Stipa comata* Trin. and Rupr.) and niggerwool (*Carex filifolia* Nutt.), was depleted in the first 2 feet by June 20. Two to eight percent available moisture persisted in the 2- to 5-foot levels. Rain amounting to 1.6 inches fell from June 27 to July 7, replenishing soil moisture in the first 2 feet of soil. Moisture content remained favorable to plant growth until the fourth week in July, but thereafter rainfall was insufficient to replenish it in the surface 6 inches until the second week in September.

Soil moisture in a wet meadow is replenished by rainfall as well as by water from the water table. The supply of ground water is a relatively constant factor, and variations in production in wet meadows from year to year result from differences in rainfall. Water is available throughout the growing season in the lower and middle portions of the wet meadows. It is obtained mostly by plant roots from the capillary fringe immediately above the water table. This extraction causes daily fluctuations of the water table. Roots in the middle portions of the meadow penetrate 2 to 3 feet into the sand where there is the necessary moisture. On the upper edge of the meadow, however, the rate of growth does not equal the rate of lowering of the water table, especially in late summer and fall. At this time plants endure periods of drought.

Both the surface 6 inches and most lower levels of a Gannet soil at Dewey Lake in 1937 contained available moisture throughout the growing season (Fig. 6).

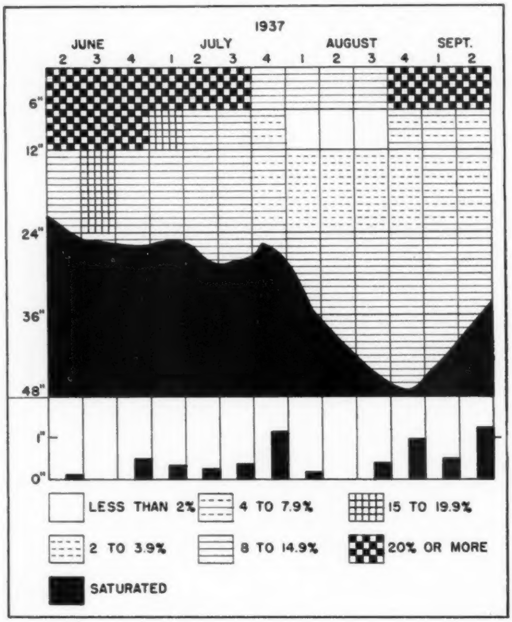

FIG. 6. Available moisture in soil in tall-grass meadow at Dewey Lake during the summer of 1937. Upper edge of the saturated zone (black) is the level of the water table throughout the season. Weekly precipitation in inches is indicated by black bars.

Available moisture in the surface 6 inches was 20 percent or more until July 22, and it never fell below 8 percent throughout the summer. The 6- to 12-inch level contained less available moisture and there was a continuous reduction of water content until heavy rains fell in the autumn. Field capacity was low in the 2- and 3-foot levels, since there was little humus or silt in the sands. Hygroscopic coefficients averaged 2.5 percent. Moisture approached field capacity immediately above the water table throughout the growing season. In an adjacent dry meadow capillary moisture was 23 to 24 inches above the water table on October 25, 1937, but in the wet meadow, such heights were not attained because of absorption by plants.

WATER TABLE AND SALT CONCENTRATIONS

The water table is subject to periodical, seasonal, and daily fluctuations. Periodical fluctuations result from cyclic occurrence of excessive or deficient precipitation in association with poor drainage. The water table at Dads Lake, where there is no surface

drainage, was nearly 8 feet below its usual level in the autumn of 1938. The water table at Dewey Lake, where surface drainage is well established, did not fluctuate more than a few feet over a period of several years. It was kept nearly normal during periods of high rainfall by surface drainage, and during drought, extreme lowering of the water level was prevented by abundant seepage and water from springs.

Seasonal fluctuations of the water table are determined by the amount of rainfall, by replenishment from the water table through springs and seepage, by loss through transpiration, and by evaporation from the lake. The water table in a wet meadow at Dewey Lake fell 1.61 feet from July 7 to August 20, 1937. It rose 0.83 feet as a result of rains in August and September, but again receded to former levels during late September, and did not return to the July level until October 22. Seasonal rise and fall of the water table is represented in Figure 6, where the zone of saturated sand is indicated. The water table fell 2.78 feet from June 30 to September 1, 1938.

Daily fluctuations of the water table regularly occur during the growing season. These fluctuations result chiefly from the quantity of moisture lost by transpiration and the rate of replenishment. Greatest fluctuations occur in the tall-grass meadow.

Water table in a tall-grass meadow near Dewey Lake fluctuated 4.4 inches during a hot, windy day (July 7) in 1937 (Fig. 7). Under moderate conditions, it fluctuated 2.3 inches on August 5, 1937, and 1.5 inches on August 12. Under conditions of high humidity, low wind, and moderate temperature on August 20, the water table fell only 0.3 inch. Fluctuation of the water table 8 feet beneath the surface of a dry meadow at Dewey Lake was 0.6 inch on August 12 and 20, 0.5 inch on September 10 and 0.2 inch on September 28. It was not determined whether these fluctuations were due to transpiration or were the result of variations in water levels in the wet meadow 100 yards distant.

During very dry weather, the most rapid lowering of the water table occurred in the morning, gradually leveling off until four to five o'clock in the afternoon after which it began to rise. During the night, it attained approximately the same level as that of the preceding morning.

Spring and river waters contain low concentrations of soluble salts. A single sample of spring water had 122.1 parts of soluble salts per million of water (ppm.). These waters present a habitat with a flora considerably different from lake waters which have a higher salt content. Salt concentrations differ from lake to lake according to drainage. Beaver, Red Deer, Hackberry, and Dewey Lakes have good surface drainage, and moderate contents of soluble salts (Beaver Lake has 235.8 ppm.). These lakes have a luxuriant growth of various pondweeds. Growth of seed plants, however, is completely inhibited in Clear Lake (13,503.1 ppm.) and in Alkali Lake, where salts have accumulated over long periods of time as a result of high evaporation, abundant run-in water, and

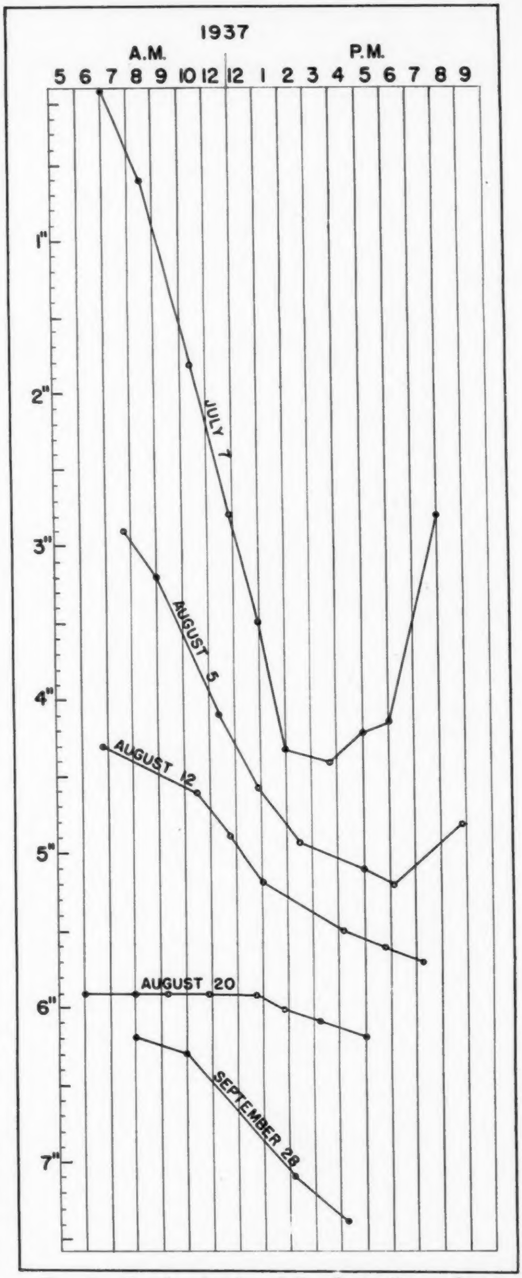

FIG. 7. Graphs showing daily fluctuations of water table in tall-grass meadow near Dewey Lake at various times during the summer of 1937.

poor drainage. High concentrations of salt, however, occur only in the lake body itself. The ground water deep beneath the bed of the lake and under the lake shores has little salt accumulation (282.9 ppm. at Dads Lake).

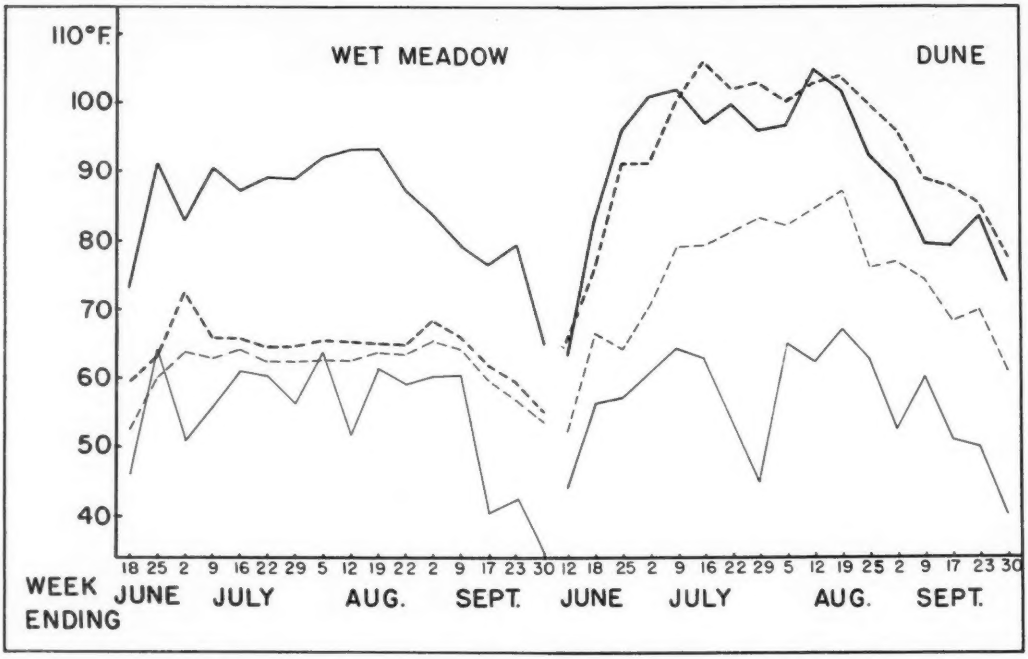

FIG. 8. Summary of average weekly minimum and maximum air temperatures three inches above the soil surface and soil temperature three inches below the surface from a wet meadow and the south slope of a dune at Valentine Lakes Refuge in 1937, respectively. Continuous lines indicate air temperatures and broken lines, soil temperatures.

Temperature of Air and Soil

Daily maximum and minimum soil and air temperatures averaged by weeks are recorded in Figure 8. Highest temperatures occurred from the first week in July to the middle of August. Average weekly maximum temperatures above 95° F. persisted for 9 weeks in both 1936 and 1937, but for only 5 weeks in 1938. There were 5 weeks in 1936 with average maximum temperatures above 100° F., but only 2 weeks in 1938. Maximum temperatures ranged from 100° to 115° F. Average maximum temperature of the mixed prairie from May to September, 1936, was 96°, and from May 20 to Sept. 9, 1938, it was 87° F. On the south-facing slope of a dune, from June 12 to Sept. 30, 1937, the average maximum temperature was 87.7°, and from May 20 to Sept. 9, 1938, it was 88.5° F. During 1938, temperatures were approximately the same on the south side of the dune and in the mixed prairie, but the mixed prairie had lower average temperatures during rainy periods.

Average daily maximum temperatures in a grove in 1936 and in a wet meadow in 1937 were persistently lower than those of the mixed prairie and the south side of a dune. Differences as great as 12° F. were recorded in average maximum daily temperatures between woodlands and mixed prairie areas in 1936, and 19° between the wet meadow and the south slope of a dune in 1937.

Night temperatures were low, and during the warmest periods, they were seldom high enough to be uncomfortable. Average minimum temperatures on the dune from June 12 to September 30, 1937, and from May 20 to September 9, 1938, were 54.4° and 60.9° F., respectively. Those of the mixed prairie in 1936 were 59.7° and 61.5° F. in 1938.

In uplands, maximum soil temperature was usually slightly below maximum air temperature, but the depression of minimum soil temperatures during the summer was never as great as that of the air. Average maximum weekly soil temperatures on dune from May 20 to September 9, 1937, and from June 12 to September 23, 1938, were 91.3° and 87.5° F., respectively. Those in the wet meadow in 1937 were 64.2° and 61.8° F. Average differences between minimum and maximum air temperatures on the dune in 1937 were 11.7° F. and in the wet meadow, 2.4° F.

Relative Humidity

Average maximum humidity for 12 weeks (from June 18 to September 9, 1937) on the dune and in the wet meadow was 73.9 and 83.7 percent, respectively. Greater humidity in the wet meadow was largely the result of high transpiration by the tall grasses. Low relative humidity occurred in midsummer with high temperatures and drought.

Average maximum relative humidity for 12 weeks (from June 3 to August 26, 1938) on the dune and in the mixed prairie was 71 and 72 percent respec-

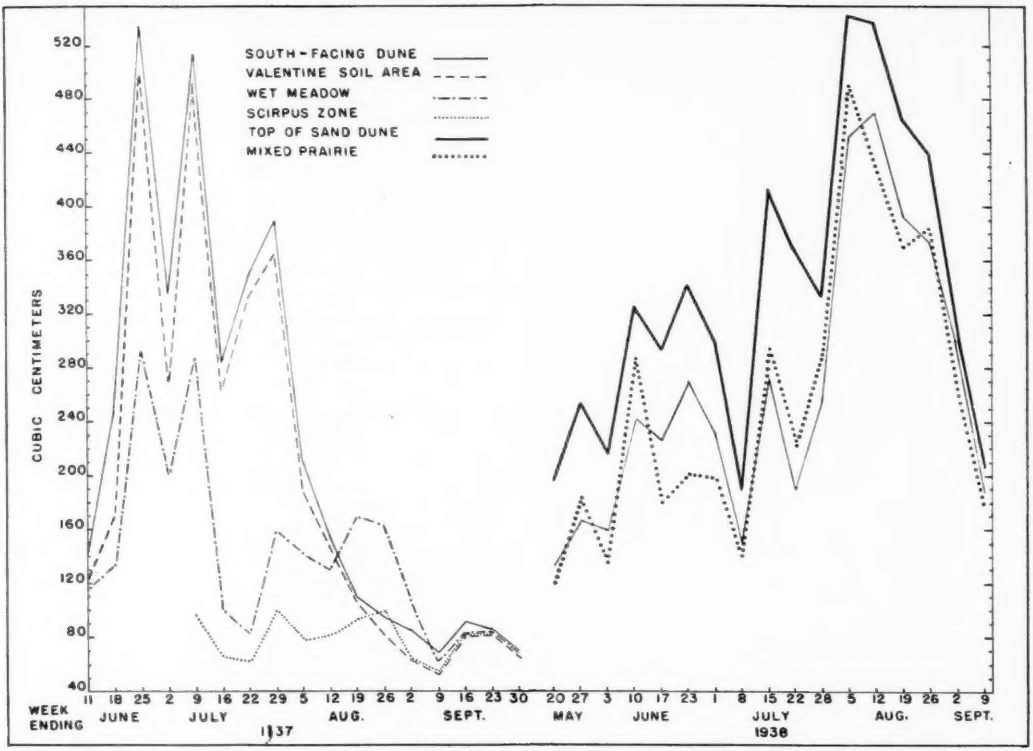

FIG. 9. Weekly rates of evaporation in several sand-hill and hardland habitats during the summers of 1937 and 1938.

tively. Average minimum humidity in the same sequence was 36 and 34 percent. Humidity was higher in the mixed prairie than in that of the dune immediately after a rain because more water evaporated from the soil on the hardlands. Average relative humidity in the several habitats at 3 P.M., June 22 to July 8, 1936, was as follows: sedge meadow, 34 percent; tall-grass meadow, 31; grove of hackberry trees, 26; and south slope of dune, 23 percent.

EVAPORATION

Weekly rates of evaporation in 1937 and 1938 are summarized in Figure 9. Average daily evaporation in 1937 on the south slope of a dune was 33.7 cc.; in dry meadow, 26.0; and in wet meadow, 19.0 cc. Evaporation in the swamp was least, with an average daily rate of 12.4 cc. Average daily evaporation during 1938 on the south slope of a dune was 37.2 cc.; on a north slope it was 29.5 cc.; and on the top 46.9 cc. Evaporation on the mixed prairie was nearly the same as that on the south slope of the dune with an average of 37 cc. Evaporation was highest on the top of the dune where currents of air moved unimpeded in all directions. High rates of evaporation occurred during periods of drought. Reduced evaporation during the last two weeks in August in both 1937 and 1938 was the result of rainfall and seasonal decrease in temperatures. Evaporation in the mixed prairie habitat was lower than that on the south slope of the dune during rainy periods. The prairie, however, had a more severe aerial environment than did the south slope of the dune during periods of drought.

WIND

Greatest wind erosion occurs during winter. Blowouts develop on the northwest side of a dune, and deposition is on the southeast side. The height to which winds blow the sand is limited and seldom exceeds 50 feet. In a blowout at Dewey Lake, the major wind movement was around the southeast side of the highest point rather than upward and over the dune. The sides of a young blowout are steep, but as erosion continues the dune becomes streamlined, permitting movement of wind over an elevation with a minimum of friction. Stakes driven on the eroding side of a young blowout in the fall marked the removal of 9 inches of sand during the winter of 1937-38.

Plants cannot revegetate a denuded area where wind erosion is severe. A complete cover of vegetation is possible only when the blowout has matured. Erosion increases when the cover of vegetation is destroyed by heavy grazing, and deposits of fine sand

are made in the meadows. Though the effects of this deposition are not immediately noticed, many wet meadows have been filled with 8 to 10 feet of fine sand in relatively recent times, as is indicated by many layers of soil buried deep beneath deposits of fine sand. Blowouts often develop when vegetation is weakened by grazing and trampling. This is especially evident around watering places everywhere in the hills.

Woodlands have a marked effect upon wind velocity, but in grassland, topography is more important in creating local differences in wind movement than is vegetative cover. During 1937, average weekly wind movement on the mixed prairie was 608 miles, but in the woodlands only 76 miles. Extremes on the mixed prairie varied from 482 to 857 miles per week, and at the woodland station 44 to 112 miles. Wind velocity was greater at the tops of dunes than elsewhere, and had a marked effect upon composition of the vegetation. Wind movement on the south side of a dune in 1937 averaged 324 miles per week; in a wet meadow the average was 288 miles. During 1938 on the south slope of a dune the average was 295 miles, and on the mixed prairie it was 272 miles. Extremes of weekly average wind movement on the south side of a dune in 1937 ranged from 105 to 728 miles and in 1938, from 102 to 504 miles. On the mixed prairie in 1938, weekly wind movement varied from 143 to 544 miles.

Light

Full sunlight at 2 P.M. late in summer was somewhat more than 10,000 foot candles. Approximately, only 1 percent of the total sunshine reached the soil in the tall-grass community and only 6 percent was recorded at a foot above the soil surface. Nowhere in the mixed prairie or on the dunes during drought years was light sufficiently low to retard plant growth; but with abundant moisture, tall grasses shaded the shorter ones considerably.

More sunlight reached the soil covered with swamp vegetation than the soil in the tall-grass meadow. An average of several readings in a dense stand of arrowhead was 15 percent of full sunlight; it was 17 percent in a mixture of arrowhead and western bulrush. In the common reed zone with an underlayer of arrowheads, light intensity was the same as that near the soil surface in the tall-grass zone. In pure stands of common reed, intensities of 2.8 to 5 percent were recorded at the surface, and 5 feet above the ground readings ranged from 8 to 24 percent.

Light values in shade of hackberry trees approximated 3 percent of full sunshine; in a willow thicket, 0.1 percent; and in a plum thicket, 2.6 percent.

GENERAL DISTRIBUTION OF VEGETATION

Cherry County is a great tract of sand-hill grassland. This is some of the best range land in the United States. The great monotony of rolling dunes and waving grass is occasionally broken by a broad, shallow valley. Here large areas of tall-grass meadow stand in contrast to smaller ones of dark-green swamp or shallow lake. Sometimes there is a grove of cottonwoods planted by the pioneers. Hardland and river-valley habitats are of minor importance, but of great interest since they have an entirely different vegetation.

The various plant communities are distributed largely according to the quantity of water available to vegetation. They are therefore described in order of succession from the submerged plants in lakes and ponds to the climax communities on the hardlands. Intermediate groups include communities of swamps, wet meadows, and sand dunes. Postclimax woodland and chaparral are present in the river valleys. The xerosere is almost absent.

Submerged and floating vascular plants grow in the lakes and ponds. Emersed hydrophytes occur in shallow water along the protected shores. There are also several characteristic hydrophytes in swamps where peat has accumulated in large quantities. Mesophytic grasses grow in the subirrigated meadows, which are conveniently divided into three zones. A lower zone, usually flooded in spring, has a growth of sedges and hydrophytic grasses. The tall grasses dominate a middle zone, and the xerophytic plants of the true prairie occur on the upper edge of the meadow where vegetation undergoes periods of drought, especially in late summer. Halophytes are present in saline meadows.

Postclimax tall grasses grow in the dune sands. Pioneer grasses are characteristic of the blowouts. As the communities mature the pioneers are succeeded by more xerophytic dominants. In the final communities, resulting from decrease in moisture, the dominants are distributed in several alternes according to minor differences in environment. Growth of tall grasses is retarded or prevented by the extreme aerial environment on top of the dunes where short grasses are dominant. Certain tall grasses occur mainly on the south slopes of dunes; others are present mainly on the north slopes. Marked changes in composition of vegetation are caused by grazing.

Mid and short grasses of the mixed prairie association occur on the hardlands, where they develop as the climax vegetation. Here also the several major species occur in communities distributed according to minor differences in environment, or composition is modified by different intensities of grazing.

Deciduous trees and shrubs form woodland and chaparral in well drained, subirrigated areas along streams, bottoms of deep canyons, and other habitats favorable to postclimax arboreal species. Groves of ponderosa pine occur on rough, stony land in the deep valleys.

HYDROPHYTIC COMMUNITIES

Plants Submerged or with Floating Leaves

Submerged and floating species are found in fresh-water lakes and in ponds formed by dams

across small streams. Several species grow from the edge of the permanent water line far into the shallow lakes. Submerged plants are able to withstand wave movement and therefore occur throughout the lakes except as inhibited by unfavorable depths, excessive saline content of water, or extremes of wave movement along unprotected, sandy shores. Near the edge of the permanent water line of protected lagoons, submerged plants become more common than the floating species.

Among the common submerged species are five pondweeds, namely, *Potamogeton pectinatus* L., *P. natans* L., *P. richardsonii* (Benn.) Rydb., *P. zostriformis* Fernald, and *P. foliosus* Raf. Hydrophytes equally as common are coontail (*Ceratophyllum demersum* L.) and milfoil (*Myriophyllum spicatum* L.).

Other pondweeds (*Potamogeton praelongus* Wulfen., *P. angustifolius* Berch. & Presl., **P. strictifolius* A. Benn.) are of less common occurrence since they grow mainly in fresh water. Other members of this group are *Najas flexilis* (Willd.) Rostk. & Schmidt., *Ranunculus delphinifolius* Torr., **Batrachium divaricatum* (Schrank) Wimmer, *Lemna trisulca* L., *Wolffia columniana* Karst., **Elodea canadensis* Michx., and *Utricularia minor* L.

Floating and partially submerged plants which are unable to withstand severe wave movement form small communities in well protected areas. The broad-leaved pondweeds and yellow cow lily (*Nuphar advenum* Ait.) are the most common constituents of such communities. The yellow cow lily, which may occur in colonies of several square yards, spreads by means of starch-laden rhizomes several inches in diameter. It has floating and emersed leaves and flower heads that usually extend well out of the water. White water lily (*Nymphaea odorata* Ait.) has been introduced in some localities. *Polygonum amphibium* L. occurs in a few places, and duckweed (*Lemna minor* L.) floats in masses upon quiet waters.

* Species marked with an asterisk are found only in water with little salt in solution.

FIG. 10. Transition zone between communities of wild rice *(Zizania aquatica)* and cattail *(Typha latifolia)*, with yellow cow lily *(Nuphar advenum)* in the center. Tops of the swamp willow *(Salix petiolaris)* appear in the background above the wild rice.

Wild rice (*Zizania aquatica* Hitchc.) is a pioneer annual species. It grows in small, protected lagoons of only a few acres where depth of water does not exceed 2 to 3 feet in the early part of the growing season (Fig. 10). It germinates under water, passes through a submerged and floating stage, and finally emerges during July and August. The plants grow 2 to 4 feet high where aeration of the soil is poor, but attain a height of 7 to 8 feet where the water table is several inches beneath the surface. Under such conditions a single plant may spread over as much as 4 square meters and produce 25 culms. Seeds fall to the ground immediately upon ripening and are a valuable food for aquatic fowl. Wild rice is not successful in competition with established marsh vegetation or annual weedy plants which germinate along the exposed lake shores when water levels fall in June and early July. Neither is it capable of surviving in open, shallow waters where the plants are subjected to the full force of wind and wave movement.

SPECIES OF THE SWAMPS

Emergent plants form well defined zones from the edge of the permanent water line to the lower margin of the tall-grass meadow. This zonation is the result of differences in the ability of the several swamp plants to withstand deficiency of oxygen. The level of the water table and time of submergence of surface soils directly affect the quantity of oxygen available to plant roots. The common species of the swamp are able to withstand fluctuations of the water table of approximately 3 feet, but they vary among themselves in survival when flooded. Common reed (*Phragmites communis* Trin.) is least able to grow in deep water, and western bulrush (*Scirpus acutus* Muhl.), swamp sedge (*Carex lacustris* Willd.), cattail (*Typha latifolia* L.), and arrowhead (*Sagittaria latifolia* Willd.) are increasingly able to grow in deep water in order named.

Depth of the water table in June and September in the various swamp zones at Dewey Lake is shown in Table 1. The upper portion of the swamp was flooded only during the early part of the growing sea-

TABLE 1. Depth of water table expressed in feet (′) and inches (″) in various plant zones at Dewey Lake in 1938.

Community	Distance ot level of water from the surface	
	June 7, 1938	Sept. 21, 1938
Wild rice—cow lily zone	3″ above	¼″ above
Wild rice—cattail transition	2′ 9″ above	1″ below
Cattail—Scirpus transition	2′ 7″ above	2″ below
Near center of the Scirpus zone	1′ 1″ above	1′ 8″ below
Scirpus—sedge meadow transition	At surface	2′ 4″ below
Sedge meadow—tall-grass transition	11″ below	2′ 11″ below
Tall grass—true prairie transition	2′ 7″ below	4′ 9″ below
True prairie—dune tall grass transition	4′ 1″ below	6′ 3″ below
Dune tall-grass community	5′ 10″ below	8′ below

son, but the arrowhead-cattail zone immediately adjacent to the permanent water line was flooded throughout the summer. The range of elevation from highest to lowest levels of the swamp at Dewey Lake was 28 inches. The water table fluctuated nearly 3 feet from spring to fall.

Arrowheads grew in nearly pure stands and formed communities with cattails on the lower edge of the swamp near the permanent water line (Fig. 11).

FIG. 11. Arrowhead *(Sagittaria latifolia)* with pondweeds (*Potamogeton* sp.) and duckweed *(Lemna minor)* floating on the water in a pond near Valentine.

They also formed a ground layer in the bulrush and common reed communities at higher levels. They were good pioneers along shores made bare by receding water levels. Here they grew from seed and produced flowers in two months. At Dewey Lake they withstood 2 to 3 feet of flooding in late May and early June. Floating leaves were present when water levels were high, but emergent leaves developed as the water table lowered. Large white flowers appeared late in June, and seeds soon matured on the pistillate inflorescences. Fleshy tubers formed late in summer, 4 to 6 inches beneath the surface. The leaves turned yellow, and the plants became dormant long before killing frosts.

Cattails are not as common as arrowhead along the lake shores. Typha formed colonies among the arrowheads in the lower portions of the swamp and occurred in all the hydrophytic communities. Typha spreads by rhizomes 8 to 10 inches in length and forms dense, compact stands under optimum environments.

Carex lacustris, also spreading by rhizomes, sometimes formed communities of several acres but more commonly they covered only a few square yards. Few other species occurred, but occasional plants of *Urtica* sp. and *Polygonum coccineum* Muhl. were present. This sedge grows in small bunches with a basal area of approximately one square decimeter. The stems are triangular with dark green, shiny leaves. Height varied from 36 to 56 inches. Flowering stalks rarely developed. Occurrence of this sedge only in the portions of the swamp where there were many springs indicated its intolerance of salinity.

Western bulrush dominated the upper portions of the swamp where maximum water table levels flooded the surface of the peaty soil from a few inches to 3.6 feet in depth. It withstood an annual fluctuation of the water table of 3 feet, and was also tolerant of moderately saline water. At Dewey Lake it dominated several acres but occurred sparingly in communities of cattail and common reed. Bulrush propagated by rhizomes a few inches to 6 feet in length, from which cylindrical culms arose every few inches. These attained a height of 4 to 6 feet. Growth began during the first week in May, 1938, and during the first week in June the stems were 3 to 4 feet tall. Inflorescences developed near the top of the stalk late in May.

Common reed grew in large colonies on the upper portions of the western bulrush zone. During periods when the water table was low it spread rapidly by extensive rhizomes, some of which attained a length of 30 feet. Culms appeared at intervals varying from 6 to 18 inches. Maximum spread was made during 1937, but under the influence of high water levels during 1938, the common reed zone receded 8 to 10 feet along the lakeward side. Growth began in the middle of May, 1938; by the first week in June culms were 30 to 36 inches tall, and each had 5 to 6 leaves. By the end of June the plants attained a height of 72 inches, and each had 12 to 13 leaves. Flowers developed on culms 7 to 8 feet high during the second week in August. In late summer the lower leaves turned yellow and fell to the ground. Widely spaced plants of arrowhead and western bulrush grew beneath the common reed.

PLANTS ABOUT SPRINGS

In the Niobrara Valley and along the shores of a few sand-hill lakes, especially those at the source of streams, are areas which are well drained and supplied with a fairly constant flow of fresh, cool water. Here the water table fluctuates but little. Much organic matter has accumulated in the moist sands. Such habitats support a large number of species of limited importance.

Scirpus fluviatilis (Torr.) A. Gray, *S. validus* Vahl., *Alisma subcordatum* Raf., and *Sparganium eurycarpum* Engelm. are found in the more hydrophytic areas where fluctuations of the water table

are moderate (6 to 18 inches). Sedges and hydrophytic grasses dominate the few small swamps where the water table is just beneath the surface and where it does not fluctuate more than a few inches throughout the year. The most important of these are *Carex hystricina* Muhl. and *Glyceria nervata* (Willd.) Trin. Others occur rarely, and may be regarded as relicts. Twenty-five such species were observed.

Among the annual plants found where the perennial grasses and sedges had been destroyed by grazing were *Echinochloa crusgalli* (L.) Beauv., *Leersia oryzoides* (L.) Swartz, *Bidens cernua* L., *Lobelia syphilitica* L., *Gerardia tenuifolia parviflora* Nutt., *Impatiens biflora* Walt., and *Mimulus ringens* L.

PLANTS OF PEAT SOILS

Peat soils with a permanent water table 6 to 12 inches beneath the surface are dominated by swamp willow (*Salix petiolaris* Smith) and marsh fern (*Thelypteris palustris* Schott.). Forbs and grasses of secondary importance are *Aster umbellatus* Mill., *Calamagrostis canadensis* (Michx.) Beauv., *Eupatorium maculatum* L., *Impatiens biflora*, *Triadenum virginicum* (L.) Raf., *Mentha canadensis* L., *Lycopus hispida* Pursh., *Polygonum coccineum*, *Phragmites communis*, *Glyceria grandis* S. Wats., *Cicuta maculata* L., *Rumex patientia* L., *Carex lacustris*.

Several forbs increased greatly in the higher portions of the community during 1937 and 1938 where the water levels become lower during the severe drought. These were *Aster nebraskensis* Britton, *Oenothera hookeri* T. & G., *Helianthus grosseserratus* Martens, *Solidago serotina* Ait., and *S. altissima* L. In the lower portions of the community the pioneer forbs, *Rumex patientia*, *Epilobium densum* Raf., *Ludwigia polycarpa* Short and Peter, and *Alisma subcordatum* also increased.

During 1937 water levels fell rapidly in the Valentine Lakes leaving bare areas of peat open to invasion. As soon as the water table receded beneath the surface, annual forbs began to grow. Even after August first, seedlings of *Chenopodium rubrum* L. grew in dense stands, and attained heights from 6 to 24 inches, depending upon their age. Several hundred acres of pure stands of this species grew in the lake beds of White Water, Pelican, Willow, and Marsh Lakes during 1937. Water levels, however, were sufficiently high during 1938 to inhibit germination over much of the area formerly occupied. *Chenopodium album* L. grew in pure stands on shores which were exposed by receding water levels in early summer, and dominated areas occupied by Typha, Sagittaria, and Scirpus during 1936. *Bidens cernua* formed extensive communities on the shores of Hackberry Lake during 1938. In addition, there were various mixtures of *Polygonum pennsylvanicum* L., *P. lapathifolium* L., *Acnida* sp., and *Panicum capillare* L.

OTHER FRESH-WATER HABITATS

Certain hydrophytic plants, including *Veronica americana* Schwein., *Mimulus glabratus fremontii* (Benth.) Grant., *Nasturtium officinale* R. Br., *Catabrosa aquatica* (L.) Beauv., and *Berula erecta* (Huds.) Coville, grew partially submerged with roots established in banks along the edges of the small, spring-fed streams where flow and temperatures of water were fairly constant throughout the year.

Shallow depressions on hardlands known locally as "buffalo wallows" are usually filled with water until early summer. Submerged and floating plants such as *Macuillamia rotundifolia* (Michx.) Raf., *Marsilea vestita* Hook. & Grev., and *Eleocharis macrostachya* Britton, are found in these places. They make a rapid growth and produce seeds or sporocarps before the pools are dry in summer.

SPECIES TOLERANT TO SALT

Depth to water table is a conditioning factor in saline habitats. Salt bulrush (*Scirpus americanus* Pers.) grows on the sandy shores immediately above the water table. Salt grass (*Distichlis stricta* (Torr.) Rydb.) develops best at levels 1 to 3 feet higher, and western wheatgrass (*Agropyron smithii* Rydb.) dominates moderately saline soils not influenced by flooding. Grasses and grasslike plants of secondary importance are *Juncus balticus* Willd., *Scirpus acutus*, *Hordeum jubatum* L., *Calamovilfa longifolia*, *Panicum virgatum* L., *Muhlenbergia asperifolia* (Nees and Mey.) Parodi., *Spartina gracilis* Trin., and *Carex siccata* Dewey. Herbs in such habitats are *Ambrosia coronopifolia* T. & G., *Suaeda depressa* (Pursh) S. Wats., *Leptochloa fascicularis* (Lam.) A. Gray, *Helianthus petiolaris* Nutt., *Leptilon canadense* (L.) Britton, *Polygonum ramosissimum* Michx., *Panicum capillare*, and *Salsola pestifer* A. Nels.

Plants tolerant of salts also dominate shores of saline lakes where ground water has a very low salt content, but where marked fluctuations of periodical water levels occur as a result of poor surface drainage. Here the bunch grasses do not become established, and the annual forbs and perennial plants which propagate rapidly by long rhizomes are dominant.

Salt bulrush at Dads Lake extended from the water's edge to levels where the water table was approximately 6 feet beneath the surface. Along the lower limits of the community the plants made a rapid growth and spread by thickened rhizomes 4 to 10 inches in length over areas of several square yards. The tender, dark green leaves reached a height of 12 to 18 inches. In two meter quadrats the number of leaves averaged 765. At the upper limit of the community, growth was much less, the leaves dried in late summer, and no seed developed. Competition with annual and perennial plants was great.

Salt grass is at its best where water levels are 16 to 36 inches beneath the surface of the sand. It grows in nearly pure stands in saline meadows adjacent to poorly drained lakes. It is a pioneer on lake shores from near the edge of the minimum annual water line outward to places 6 to 8 feet above minimum water tables. It is also present in small

quantities in tall-grass meadows. Salt grass grows 2 to 8 inches in height, and spreads by long rhizomes (Fig. 12). A single meter quadrat had 2,616 stems.

FIG. 12. Salt grass *(Dictichlis stricta)* along shores of Clear Lake depicting manner of advance of plants into bare areas by rhizomes from a central, established colony.

COMMUNITIES OF MESOPHYTIC TALL GRASSES

Mesophytic tall-grass communities dominate lands where the capillary fringe above the water table is within reach of grass roots. Such conditions are found in sand-hill valleys adjacent to well drained, fresh-water lakes and along streams. Composition of meadows is modified by soil aeration, by depth to the water table, and by such coactions as grazing and mowing (Fig. 13). Growth of the mesophytic tall

FIG. 13. General view of wet meadow near Merriman, with ranch house and stacks of hay in immediate foreground and sand-hill range in distant background.

grasses is inhibited by great fluctuations of the water table and high saline content of ground water or soil.

The wet meadow has three zones of vegetation. A zone along its lower edge is flooded during the early part of the growing season. A second, more mesic zone is never flooded, but the plants always have access to ground water 2 to 3 feet beneath the surface. A third zone along the upper edge of the meadow receives moisture from the capillary fringe only during the early part of the growing season. Here plants endure periods of drought in summer and fall.

HYDROPHYTIC GRASS AND SEDGE ZONE

The lower zone was dominated by bluejoint *(Calamagrostis canadensis)* and Sartwell's sedge (*Carex sartwellii* Dewey). Less abundant grasses and sedges were *Phalaris arundinacea* L., *Scirpus americanus*, *Hordeum jubatum*, *Carex lanuginosa* Michx., *C. scoparia* Schkuhr., *C. nebraskensis* Dewey, and *C. praegracilis* W. Boott. The width of the zone varied from a few feet to 30 or more, depending upon the slope of the land adjacent to the lake or stream. At Dewey Lake the zone was flooded to a depth of 4 to 6 inches in spring. During 1938 minimum water levels ranged from 2.5 feet beneath the surface at its lower edge to 3 feet at the upper margin of the zone.

Forbs occurred only in small numbers. They were *Asclepias incarnata* L., *Lycopus velutinus* Rydb., *Triglochin maritima* L., *Cicuta maculata*, *Bidens aristosa* (Michx.) Britton, *Aster salicifolius* Lam., *Scutellaria epilobifolia* A. Hamilt., *Helianthus grosseserratus*, *Polygonum coccineum*, and *Stachys scopulorum* Greene.

MESOPHYTIC TALL-GRASS ZONE

The middle portion of the wet meadow was occupied by big bluestem (*Andropogon furcatus* Muhl.)-Indian grass (*Sorghastrum nutans* (L.) Nash) community. The major grasses, listed in approximate order of their occurrence in increasingly less mesic habitats, were slough grass (*Spartina pectinata* Link), switchgrass *(Panicum virgatum)*, Indian grass, and big bluestem. This community was found extensively in all the sand-hill valleys where maximum water table levels ranged from 0.9 to 2.3 feet beneath the surface, and minimum levels, from 2.9 to 4.9 feet. Optimum levels were at depths of 1.5 to 3 feet. Active growth in the tall-grass meadow began the first week in May in 1938. Bluejoint, redtop (*Agrostis alba* L.), and slough grass had attained heights of 4 to 6 inches, and Indian grass, big bluestem, and switchgrass were 2 to 3 inches tall by June 6. The average height of the tall grasses late in June was 10 to 12 inches. Timothy (*Phleum pratense* L.), redtop, and slender wheatgrass (*Agropyron pauciflorum* (Schwein.) Hitchc.) bloomed during the first week in July and produced flowering heads at a height of 24 to 36 inches. Meadow grasses grew poorly during the midsummer but activity was again resumed late in August and throughout September. The tall-grass dominants, which included Indian grass, big bluestem, and switchgrass, flowered and seeded during the fall.

Grasses of secondary importance occurring in well developed tall-grass communities were *Agropyron pauciflorum*, *Phleum pratense*, *Muhlenbergia filiformis* (Thurb.) Rydb., *M. foliosa* (Roem. and Schult.)

Trin., and *Sphenopholis obtusata* (Michx.) Scribn. Grasses of secondary importance which grew chiefly on the upper edge of the zone where vegetation was commonly in phases of disturbance were *Poa pratensis* L., *P. compressa* L., *P. arida* Vasey, *Agropyron smithii*, *Agrostis exarata* Trin., *Bromus inermis* Leyss., *Panicum scribnerianum* Nash, *Hordeum jubatum*, *Agrostis hyemalis* (Walt.) B. S. P., *Distichlis stricta*, and *Elymus canadensis* L.

In 1938 few forbs were present in well developed meadows at Dewey Lake. Ten vernal, 1 estival, and 10 autumnal species were recorded, however, in areas disturbed by making hay, grazing, or by burrowing animals. Prevernal herbs were absent from the tall-grass meadow.

True-Prairie Zone

Communities characteristic of the true prairie dominate the upper portions of the wet meadows and form a narrow zone of transition between the mesophytic, tall-grass communities at slightly lower levels and the less mesophytic, tall grasses on the dunes. True-prairie species also invade mesic sand-dune habitats and grow in disturbed phases of the tall-grass meadows. This community is a westward extension of the true prairie, and only the most xerophytic species of that association are present. They are readily disturbed by drought and fluctuation of the water table. Clumps of grasses are often widely spaced, and true-prairie forbs occupy the interstices. This community is usually confined to a zone where the minimum depth of the water table is between 4.5 and 6.5 feet.

Canadian wild rye *(Elymus canadensis)*, switchgrass, prairie dropseed (*Sporobolus asper* (Michx.) Kunth.), little bluestem, June grass (*Koeleria cristata* (L.) Pers.), and western wheatgrass were the grasses of primary importance in this zone. They are listed in the order of their ability to grow in increasingly xerophytic situations, the most xeric last.

Canadian wild rye grows in isolated clumps in the wet meadows, and it sometimes forms communities along the lower edge of the true prairie. It is also an early invader on stabilized dune sands, but it is unable to compete with the dominants either on the dunes or in the meadows. Its ecological habit is comparable to that of switchgrass, but it is less abundant because vegetative propagation is less efficient. Wild rye began growth late in April, flowered in middle July, and matured seeds in August. Production of forage was high in the wild-rye community.

Switchgrass has green leaves in the wet meadows, but a glaucous form is common as a pioneer in dry meadows and on the dunes where competition with the less mesophytic grasses is not severe. In much disturbed areas of the true prairie it had rhizomes 3 to 6 inches long and formed open bunches a few square feet in area. It attained a height of 3 to 4 feet in the most favorable habitats, but usually was not more than 2 feet high. Like slough grass, it was unable to compete with well established stands of Indian grass and big bluestem in the meadow.

Little bluestem was once a dominant in the sand hills, but since the great drought it is limited to the most favorable dune habitats. Development of tall-grass communities on the dunes under grazing as well as the occurrence of drought are the major reasons for its disappearance in recent years. Little bluestem also grows in the upper edge of the wet meadow, in areas receiving runoff water on the hardlands, and in the rough, stony lands in river valleys. It has a compact bunch habit, begins growth in early May, and flowers in August. No inflorescences developed in dune habitats in 1937, but in 1938 many bunches revived and flowered. No seeds developed, however. Fifty bunches were observed on a south-facing dune at Dewey Lake in 1937. Twenty-two percent of them were dead, 70 percent were partially killed, and only 8 percent suffered no loss.

June grass grows in bunches and is about 16 inches tall in fruit. It begins growth in late April and flowers about the first week in June. It is therefore more successful as a pioneer on dune sands and as a dominant in the upper zones of the wet meadows than is little bluestem. Seed production during the period of study was very low. The root system is represented in Figure 22. The fine roots penetrated to a depth of 2 feet in dune sand, but did not spread laterally as is characteristic of the dominant dune bunch grasses such as sand dropseed, hairy grama, and sand-hill lovegrass (Figs. 20, 25).

Other grasses and grass-like plants found in this upper zone are the dominants and minor species of the tall-grass community already listed. The dominants of the dunes are here at the lower limits of their distribution.

Four rhizomatous perennial forbs, prairie sage (*Artemisia gnaphalodes* Nutt.), perennial ragweed *(Ambrosia coronopifolia)*, smooth goldenrod (*Solidago glaberrima* Martens), and upland sunflower (*Helianthus rigidus* (Cass.) Desf.), are of primary importance in the true-prairie zone (Fig. 14). Prairie sage has the widest distribution.

FIG. 14. Smooth goldenrod *(Solidago glaberrima)* and prairie sage *(Artemisia gnaphalodes)* are common plants in true prairie and disturbed phases of the wet meadows in sand-hill valleys.

Twenty-five species of perennial and annual forbs are of secondary importance. The most common of the perennials include *Lepachys columnifera* (Nutt.) Rydb., *Potentilla arguta* Pursh, *Glycyrrhiza lepidota* Nutt., *Erigeron ramosus* (Walt.) B. S. P., *Psoralea argophylla* Pursh, *Amorpha canascens* Pursh, *Delphinium virescens* Nutt., *Tragopogon officinale* L., *Apocynum cordigerum* Greene, *Liatris squarrosa* Willd., *Tradescantia occidentalis* (Britton) Smyth., *Cirsium plattense* (Rydb.) Cockerell, *Solidago rigida* L., *Equisetum kansanum* J. H. Schaffner, *Lithospermum linearifolium* Goldie, *Verbena stricta* Vent., and *Pentstemon gracilis* Nutt. The annual and biennial forbs and grasses include *Festuca octoflora* Walt., *Helianthus petiolaris*, *Erigonum annuum* Nutt., *Sisymbrium altissimum* L., *Acmispon americanus* (Nutt.) Rydb., and *Ambrosia elatior* L.

The rhizome habit is well developed in the wet-meadow communities and is especially evident in disturbed phases of vegetation. In the lower portions of the meadow five out of nine grasses and grass-like plants propagate by rhizomes. Only little bluestem, big bluestem, and June grass grow in dense bunches. These species are at a disadvantage in areas disturbed by drought or by rapid fluctuations of the water table, grazing, or making of hay. They occur chiefly in the stable habitats where vegetation attains maximum development.

More than a third of the forbs in the wet meadows possess rhizomes. They are especially common among the composites. Species without rhizomes or with single stems are of secondary importance throughout the wet meadows, although they constituted 61 percent of the total list of forbs.

The relation of roots of several plants of the true-prairie to levels of the water table in late fall are shown in Figure 15. Here minimum water levels are too far beneath the surface for plant roots to penetrate the moist soil to the capillary fringe, a zone of moist sand 24 to 26 inches above the water table. It is probable, however, that water levels three feet above the minimum annual levels supply plants with moisture until the middle of July. After that time the water table lowers more rapidly than the roots elongate.

Changes occurred from 1936 to 1939 throughout the meadow at Dewey Lake as a result of drought and depletion of the ground water. There was, however, no disturbance from hay making. Tall grasses spread into the bluejoint-sedge zone; slough grass spread 30 to 40 feet to the upper edge of the swamp. Strong flowering culms attained a height of 6 to 8 feet (Fig. 16). Indian grass and switchgrass spread into the bluejoint-sedge zone along its upper edge. Sartwell's sedge, redtop, and smartweed spread in the upper edge of the swamp.

Data from permanent quadrats in the middle portions of the meadow revealed that Indian grass was the sole dominant in 1937, and only a few stems of big bluestem, forbs, and secondary grasses were present. The meadow was not cut during the three succeeding years. By 1939 the quadrats were dominated by big bluestem. Indian grass, timothy, and several minor grasses and forbs almost completely disappeared.

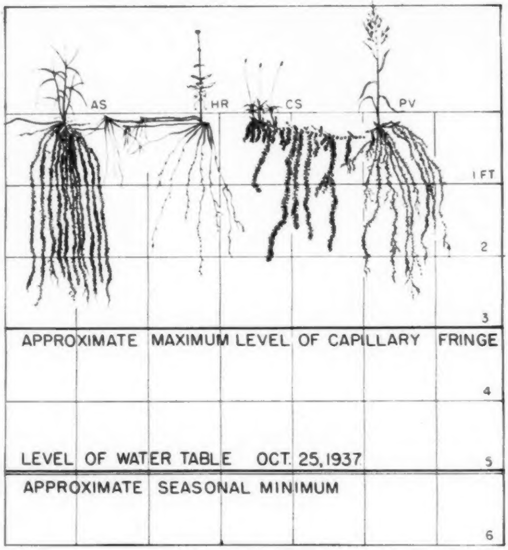

FIG. 15. Bisect showing roots of several true-prairie grasses and forbs in relation to the water table in the upper portions of the meadow at Dewey Lake in the dry year of 1937. Western wheatgrass *(Agropyron smithii)* (AS), prairie sunflower *(Helianthus rigidus)* (HR), *Carex siccata* (CS), and switchgrass *(Panicum virgatum)* (PV).

Adjustments also took place in the upper meadow. General observation revealed that the sand-dune grasses slowly increased at the expense of forbs from 1936 and 1939.

Several changes result from grazing and hay making. Prairie sage and many of the less common forbs are grazed by cattle, but perennial ragweed, blue vervain *(Verbena stricta)*, ironweed (*Vernonia*

FIG. 16. Bluejoint *(Calamagrostis canadensis)* and sedge (*Carex* sp.) community invaded during the summer of 1937 by slough grass *(Spartina pectinata)*, the tall grass in the background, as a result of rapid lowering of the water table.

fasciculata Michx.), and narrowleaved goldenrod (*Euthamia camporum* Greene) are not palatable and therefore increase in heavily grazed pastures. Beeweed (*Peritoma serrulatum* (Pursh) DC.) is an odorous, annual plant which grows in large numbers in similar situations. *Eragrostis spectabilis* (Pursh) Steud. grows in bunches 10 to 16 inches in height and forms conspicuous stands on the upper edges of meadows, being especially conspicuous in September. This grass, however, occurs mainly in areas disturbed by hay making.

TALL GRASSES ON THE DUNES

Tall grasses characteristic of sand habitats occur on the dunes and form broad ecotones with the mixed prairie of the hardlands and with the true prairie on the upper edge of wet meadows. The several sand-hill dominants are distributed in communities according to variations in aerial environment and in efficiency of infiltration of rain by the various textures of sand. They are all postclimax species. The efficiency of sand in absorbing rainfall without loss by runoff and in almost entirely preventing evaporation from its surface provides the compensating factor. This factor is especially important during summer when rainfall is limited and evaporation is high. The several communities of dune grasses vary in composition and in structural characteristics such as density of vegetation, seasonal aspects, and layering. The line of demarcation between these communities of dune grasses and the mixed prairie is somewhat indefinite, but boundary lines between them and true prairie are narrow and well defined.

Succession and Degeneration

The *Redfieldia flexuosa* community represents the earliest phases of development of sand-hill vegetation; communities of *Muhlenbergia pungens* follow somewhat later in succession. Several well developed communities in dune-sand and hardland habitats are found mainly on the Fort Niobrara Game Preserve where vegetation has been free of grazing for a long period of time. Certain winter pastures, however, have a similar composition because they are not disturbed during the growing season. Sand-hill bluestem, sand-hill lovegrass, and sand reedgrass are the main components of the fully developed communities on dune sands. Hairy grama, sand dropseed, and sand-hill sedge (*Carex heliophila* Mackenzie) are important species in the ground layer.

Species of secondary importance on dune sands are little bluestem, June grass, switchgrass, *Cyperus schweinitzii* Torr., Indian ricegrass (*Oryzopsis hymenoides* (Roem. & Schult.) Ricker), and porcupine grass (*Stipa spartea* Trin.). Mixed-prairie grasses which invade dune sands along the zone of contact in order of decreased importance are western needlegrass, blue grama, and western wheatgrass.

Most of the palatable species have been selectively grazed on most of the ranges for so long a time that they are not as numerous as the less palatable ones. The palatable species are sand-hill lovegrass, sand-hill bluestem, and switchgrass. The growth of sand reedgrass as well as hairy grama and sand-hill sedge is also reduced by grazing. The species which are less palatable or which respond quickly to increased moisture supply in disturbed communities become the dominants in disclimax communities. Sand reedgrass and sand dropseed are the most important species. On severely degenerated ranges, Muhlenbergia is the chief grass because it is not readily grazed. Degeneration of a sand-hill range thus falls into three stages; decrease of the most palatable species, dominance of Calamovilfa and sand dropseed, and finally dominance of Muhlenbergia. This is approximately the inverse order of development of vegetation.

Redfieldia flexuosa.—Since the stabilization of sand-hill habitats by control of fire and development of vegetation under grazing, the areas suited to blowout grass have been materially reduced. Blowout grass is a tall mesophytic species which grows on both the leeward and windward sides of blowouts and occasionally in severely disturbed phases of sand-hill vegetation (Fig. 17). It spreads by long, slender rhizomes which are 6 to 24 inches deep. The long, flexuous culms and leaves grow 20 to 36 inches tall. Roots occur at the nodes of the rhizomes and penetrate to a depth of 4 feet. There are numerous laterals 0.5 to 2 inches in length (Fig. 18).

FIG. 17. A general view of a community of blowout grass (*Redfieldia flexuosa*) on the leeward side of a blowout southwest of Valentine.

Redfieldia grows most actively near the bottoms of blowouts where wind erosion is reduced. The aerial environment in the blowouts is characterized by strong winds, high temperatures, and bright light, but moisture is available throughout most of the growing season, and competition for moisture is almost nil. Long, slender rhizomes spread into the unstabilized portions of the blowouts in summer, but these are exposed in winter when wind erosion is most active. Initiation of stabilization is not the result of revegetation and is possible only when the blowout has developed a streamlined, mature form.

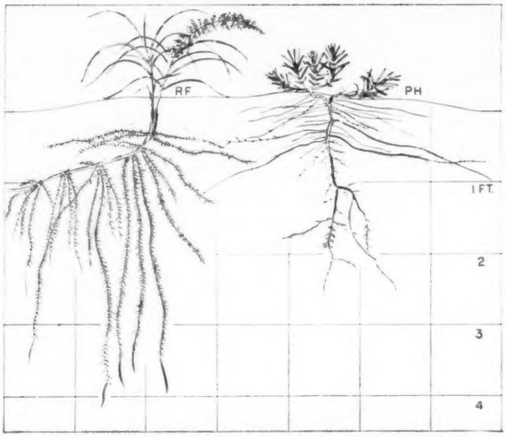

FIG. 18. Bisect showing characteristic root systems of *Redfieldia flexuosa* (RF) and *Pentstemon haydeni* (PH) in a blowout near Valentine.

This pioneer community of Redfieldia is readily displaced by more xerophytic grasses such as Muhlenbergia.

A summary of stem counts of grasses in 25 quadrats from 5 separate Redfieldia stations is shown in Table 2. Redfieldia maintained an open growth in

TABLE 2. A summary of the total number of bunches (number in parenthesis) or stems of grasses from 10 census and basal area quadrats from each of 10 stations in several phases of development of the Redfieldia and Muhlenbergia communities. The stations are listed in order of increased complexity from left to right.

	Redfieldia communities					Muhlenbergia communities				
Redfieldia flexuosa	276	812	587	714	608	140	5	27	....	....
Muhlenbergia pungens	....	....	....	71	....	190	1354	3302	902	1026
Andropogon hallii	....	....	....	....	....	81	15	2	16	44
Calamovilfa longifolia	....	....	....	....	....	....	41	26	163	86
Sporobolus cryptandrus	....	....	....	....	....	....	8	18	16	16
Bouteloua hirsuta	....	....	....	....	....	....	(1)	(4)	(33)	(126)
Cyperus schweinitzii	....	....	....	....	....	....	3	....	7	14
Carex heliophila	....	....	....	....	....	....	....	8	10	6
Stipa comata	....	....	....	....	....	....	....	(2)	....	....
Koeleria cristata	....	....	....	....	....	....	....	(14)	(4)	(3)
Aristida longiseta	....	....	....	....	....	....	....	....	3	....
Andropogon scoparius	....	....	....	....	....	....	....	....	(4)	(31)
Eragrostis trichodes	....	....	....	....	....	....	....	....	(1)	....
Total basal cover in sq. cm.	130	400	255	390	308	344	1424	1810	914	2631

the first stages of development, but as succession proceeded both the number of stems and number of species increased. Perennial forbs were *Rumex venosus* Pursh, *Pentstemon haydeni* S. Wats., *Comandra pallida* A. DC., *Phaca longifolia* (Pursh) Nutt., *Oenothera albicaulis* Pursh, *Lygodesmia juncea* (Pursh) D. Don., and *Petalostemon villosus* Nutt. Sixteen species of annuals were also found. These were widely spaced, and those which maintained short, prostrate growth were the most numerous. With the exception of *Rumex venosus*; *Pentstemon haydeni*, *Oenothera albicaulis*, and *Phaca longifolia*, all the forbs persisted in the Muhlenbergia stage of development, but only Psoralea and Lygodesmia were found in the well developed dune communities. Many of the annual forbs also occurred only in the Redfieldia community. Basal cover from 25 quadrats averaged about 0.5 percent of the total area. Redfieldia is not readily grazed during the growing season, but since it remains green for a time after other dune grasses have become tough and dry, it is utilized by cattle in the fall.

Muhlenbergia pungens.—Sand-hill muhley is a pioneer on relatively stable dune sands and acts as a successor to Redfieldia because of its more compact growth and efficient root system (Fig. 19). Pioneer

FIG. 19. Sand-hill muhley *(Muhlenbergia pungens)* growing on dune sand. (Photograph by J. E. Weaver.)

colonies of sand-hill muhley often completely cover areas of a few to several square feet. These catch the blowing sands and further stabilize the habitat. The pioneer bunches grow most luxuriantly. As the dominant grasses increase, sand-hill muhley is weakened and disappears entirely from the tall-grass communities. It becomes a permanent part of sand-hill vegetation only on tops of dunes where absorption of rain is at a maximum, but where aerial environment is more severe than in any other dune habitat.

The leafy, prostrate, rhizomatous culms are 4 to 6 inches in length, and 3 to 4 are produced each spring from the perennial portions of the culms of the preceding year. Vigorous plants develop one to six new roots per stolon each year during early June. In weak plants, new growth depends upon roots already established. The roots of primary rank attain a length of 3 to 4 feet, but the laterals are not numerous and are widely spaced (Fig. 20). The roots, which approximate a millimeter in thickness, are unable to deplete soil moisture rapidly.

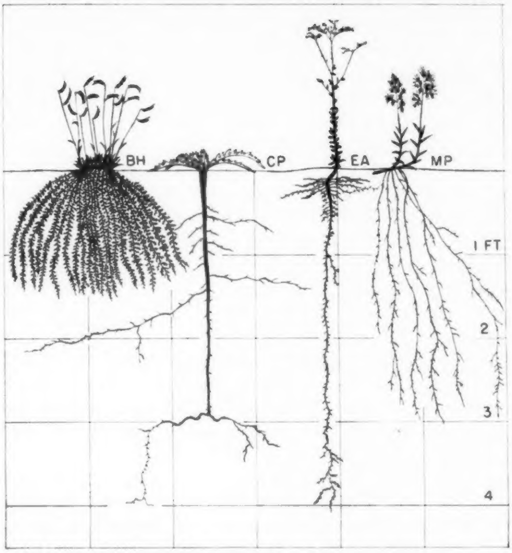

FIG. 20. Bisect on top of dune showing general form of root systems of several species in the sand-hill muhley-hairy grama community. *Bouteloua hirsuta* (BH), *Cirsium plattensis* (CP), *Eriogonum annuum* (EA), and *Muhlenbergia pungens* (MP).

The glaucous, stiff leaf-blades are from 1 to 2 inches in length and 9 to 13 are usually present per culm. They are not readily grazed, and consequently the grass thrives in areas disturbed by grazing. Reddish inflorescences, 10 to 14 inches in height, are produced throughout the summer whenever there is a sufficient water supply. Where competition is not great, production of seed is abundant.

The several Muhlenbergia communities are arranged in order of increased complexity in Table 2. The first four stations were on the Valentine Lakes Refuge where grazing had kept dune vegetation in early phases of development. The fifth was on the Fort Niobrara Game Preserve where the dunes had not been disturbed by grazing since 1914. Early development of the community is characterized by an increase in number of species of grasses and forbs as well as in number of plants. Late development is indicated by the disappearance or decrease of pioneer perennial grasses and forbs and nearly all of the annual species. The dominant grasses increase. These changes are caused largely by competition for moisture. Basal cover also increased with maturity of the community. In an early phase of development it averaged 82 square centimeters per quadrat, but in a final phase, 526, an increase of 540 percent. Basal cover, as a result of the bunch habit and prostrate growth of the dominants, was 2.7 percent higher than in any other dune community.

Andropogon hallii.—Sand-hill bluestem is a tall grass which is a common pioneer in blowouts. As a pioneer it is exceeded only by Redfieldia and Muhlenbergia. Mature communities occur in somewhat more mesophytic dune habitats than either the mature stands of sand-hill muhley and hairy grama on top of the dunes or those of Calamovilfa on the lower portions of the south slopes. This is a habitat where the winds are ameliorated somewhat by topography and where the sand texture is coarser than that at lower portions of the dune. Mature Andropogon communities also are found on the tops of low, rolling dunes or in local areas of coarse sand.

Calamovilfa is a common codominant, but it attains neither the height nor density of sand-hill bluestem. Hairy grama is the most important species in the ground layer. It produced twice as much forage as the sand-hill sedge, sand dropseed, little bluestem, and June grass, the other members of the ground layer. Muhlenbergia and two mixed-prairie species, western needlegrass and blue grama, occurred in small quantities. The Andropogon community had 20 percent less basal cover than that of sand-hill muhley. The leaves of sand-hill bluestem are readily grazed by cattle, and therefore this species is not common on the heavily grazed ranges.

Sand-hill bluestem grew 3 to 5 feet tall and had 6 to 9 glaucous, tender leaves per culm. The blades approximated 1 centimeter in maximum width and often attained a length of 14 to 16 inches. Growth began early in May, and flowering took place from the first week in July until September, according to the occurrence of rain. Seeds were seldom formed in well developed communities.

Sand-hill bluestem maintained an open growth in the mature communities, but in the blowouts it formed dense branches. In the former, the rhizomes were 4 to 8 inches in length, but in the blowouts they did not exceed 4 inches. This is an adjustment to differences in competition for water. Rhizomes made their greatest growth in spring, and roots originating from the nodes late in May penetrated to depths of 4 to 6 feet. An average of 14 roots per rhizome was found on well developed plants by August, 1938.

Eragrostis trichodes.—Sand-hill lovegrass grows on north slopes of dunes where it is protected from desiccating south winds (Fig. 21). The most mesic and most extensive communities are found on the highest dunes. It forms a narrow ecotone with the Calamovilfa community near the bottom of the dunes, and on the upper portions it is mixed with Andropogon and Muhlenbergia. Since it is highly palatable the stand cannot be maintained under summer grazing. Lovegrass is slow to invade blowouts, but easily supplants Muhlenbergia and hairy grama once invasion begins.

Sand-hill lovegrass grows in widely spaced bunches. At Fort Niobrara where an average of 7 bunches were present in each quadrat, the average basal cover per bunch from 25 quadrats was 25 square centimeters. At Valentine Lakes Refuge the average from 12 quadrats was 21.7 square centimeters. The reddish-green blades were about 1 cm. in width and rolled tightly during periods of drought. Five to seven leaves 8 to 16 inches in length were present on each culm, and the inflorescences, under favorable condi-

FIG. 21. Sand-hill lovegrass *(Eragrostis trichodes)* in open dune-sand area showing its bunch habit and flowering culms.

tions, attained a height of 30 to 40 inches. An abundance of seed developed at Valentine Lakes Refuge after the fall rains of 1937 and 1938.

The roots did not penetrate beyond a depth of 18 inches, but spread 18 to 30 inches laterally (Fig. 22). An average of 13 roots originated from each new

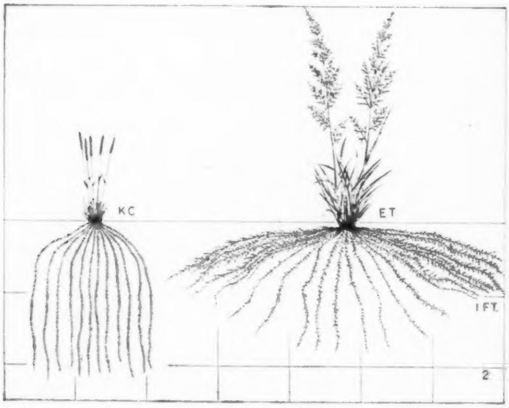

FIG. 22. Bisect showing general form of root systems of June grass *(Koeleria cristata)* (KC) and sand-hill lovegrass *(Eragrostis trichodes)* (ET) on north-facing side of dune at Fort Niobrara.

rhizome in 1938. The small roots are numerous and thoroughly spread through the surface sands.

The well developed community of lovegrass excludes both the short bunch grasses and the tall grasses. In the disturbed community, however, the tall grasses of dunes and the short bunch grasses were dominant. Three bunch grasses (lovegrass, western needlegrass, and little bluestem) had only 9.3 percent of the basal cover they occupied in the climax community, but in the disclimax community hairy grama and June grass had 446 percent more bunches. The dune tall grasses (sand reedgrass, sand-hill bluestem, and switchgrass) had 60.5 percent more culms.

Calamovilfa longifolia.—Sand reedgrass is the most characteristic grass of the sand hills. It grows in a wide range of habitats from the coarsest dune sand to the very fine sandy loams, but it makes its best growth on the south slopes of dunes and the broad, dry valleys (Fig. 23). Codominants vary according to sand texture and the degree of grazing. Hairy grama, blue grama, and western needlegrass are the major codominants in well developed communities, but on dunes sand dropseed is the major one in disturbed phases caused by grazing, and on fine sands, especially in the dry meadows, blue grama is the major codominant under grazing.

FIG. 23. Sand reedgrass *(Calamovilfa longifolia)* on the left and sand dropseed *(Sporobolus cryptandrus)* on the right on Valentine sand in a dry meadow at Dewey Lake.

Calamovilfa attains a height of 30 to 40 inches. The best developed culms had 10 to 12 glaucous, fibrous leaves with blades 15 to 20 inches long and nearly a centimeter wide. The leaves roll readily when moisture is not available. They withstand long periods of drought, but quickly revive upon receiving moisture. Development began late in April or early in May, and much growth was made during spring. Flowering occurred from July to September, but formation of seed was usually confined to plants growing in disturbed areas where moisture was more abundant.

Sand reedgrass propagates almost entirely by rhizomes. One to five new rhizomes per culm developed in May and June. They varied in length from 3 to 10 inches, and remained dormant until the following spring when a single culm and several new roots developed from each rhizome. A few roots, however, developed shortly after the rhizomes began to grow. Rhizomes excavated August 18 had an average of 13 roots each. These roots were nearly 4 feet long and 2 to 3 mm. in diameter, except at the starch-laden tips where they were sometimes 10 mm. in thickness (Fig. 24).

In pure stands of Calamovilfa, basal cover was low, with a total of only 1 percent, but where the bunch grasses were present it was greater. Where it accompanied sand reedgrass and hairy grama, basal cover was 2.5 percent, but where it occurred with blue grama a cover of 1.9 percent was found. Where sand reedgrass was codominant with needlegrass, the cover was 4.4 percent.

The sand reedgrass-hairy grama community grows on the tops of broad, low dunes where movement of wind is not as great as on the tops of high ones. The ground layer of bunch grasses comprised 27 percent of total plant units (that is, stems or bunches) and 89 percent of the basal cover.

The sand reedgrass-blue grama community (Table 2) represents a transition toward the hardlands where neither the short-grass nor the tall-grass dominants made their best growth. Here, however, Calamovilfa was most important. It comprised 25.6 percent of the basal cover but occupied only 1.9 percent of the area. Among the grasses of secondary importance, sand dropseed and sand-hill bluestem ranked second and third in basal cover. Sand-hill sedge and blue grama formed a ground layer beneath the tall grasses.

In ungrazed areas on Fort Niobrara Game Preserve the *Calamovilfa longifolia-Stipa comata* community occurs on the harder portions of the sand hills, especially in the Valentine soil areas where hygroscopic coefficients are 3.0 to 3.5 percent. Sand reedgrass and needlegrass completely excluded blue grama, and sand dropseed occupied a place of secondary importance. Basal cover was 4.8 percent. Needlegrass composed 64 percent of total basal cover and was followed in importance by sand dropseed, sand reedgrass, and sand-hill lovegrass in the order named.

Sporobolus cryptandrus.—Sand dropseed is a pioneer in abandoned fields of fine sandy loams and grows in small quantities in disturbed phases of the mixed prairie, but it does best on sand-hill range where it is codominant with sand reedgrass (Fig. 23). It maintains itself in climax vegetation as a dominant only in a zone of transition where thin layers of sand overlie fine sandy loams, and is present in small quantities throughout the well developed sand-dune communities.

Sand dropseed has an open bunch habit. The culms attained a height of 3 feet under favorable conditions of moisture during late August or early September, but with a smaller water supply the height was only 1.5 to 2 feet. Growth began in late April or early May. By the middle of May 1938, 3 or 4 green leaves were present per culm, and on August 30, an average of 9 was recorded on well developed plants. The leaf blade was 7 to 8 inches in length. At Fort Niobrara in 1938 and 1939, flowering took place during the first two weeks of September, but in 1937, during the last week of August. The inflorescences elongated beyond the sheath under conditions favorable to growth. An abundance of seed developed every year. It is by prolific seeding that this species is able to maintain itself as a pioneer and as a disclimax species.

Sand dropseed has a shallow root system which utilizes light summer rains effectively (Fig. 25). The main roots were a millimeter in diameter, attained an average length of 18 to 24 inches, and had a maximum length of 36 inches in the blue grama-sand dropseed community. These with their fine branches thoroughly occupied the surface foot of sand in 1938. The number varied from 3 to 10 according to the vigor of the individual plant.

Carex heliophila.—Sand-hill sedge is common in well developed vegetation where it attains a height of 3 to 6 inches. About 16 plants per quadrat were present in the sand-hill bluestem community; 17 in the sand reedgrass community; and 19 in the community dominated by sand reedgrass and blue grama. This sedge is less conspicuous on the top and north slopes of dunes and is seldom found in the mixed prairie, where it is regularly replaced by *Carex filifolia*. It is not abundant on range land. An open growth results from development of stolons 4 to 8 inches long. Fine roots penetrate into the sand 8 to 16 inches. Growth begins early in April, and seeds mature by the first week in June. It is semidormant during summer but revives in the fall when moisture is present and temperatures moderately low.

Forbs on Sand Dunes

Forty-eight perennial forbs were recorded on the sand dunes, but only five were of much importance. In addition, 3 biennials, 19 annuals, 3 cacti, and 6 half-shrubs were present. The average number of forbs from 25 quadrats in well developed sand-dune communities was 8. The sand-hill muhley-hairy grama community had about 19 forbs per

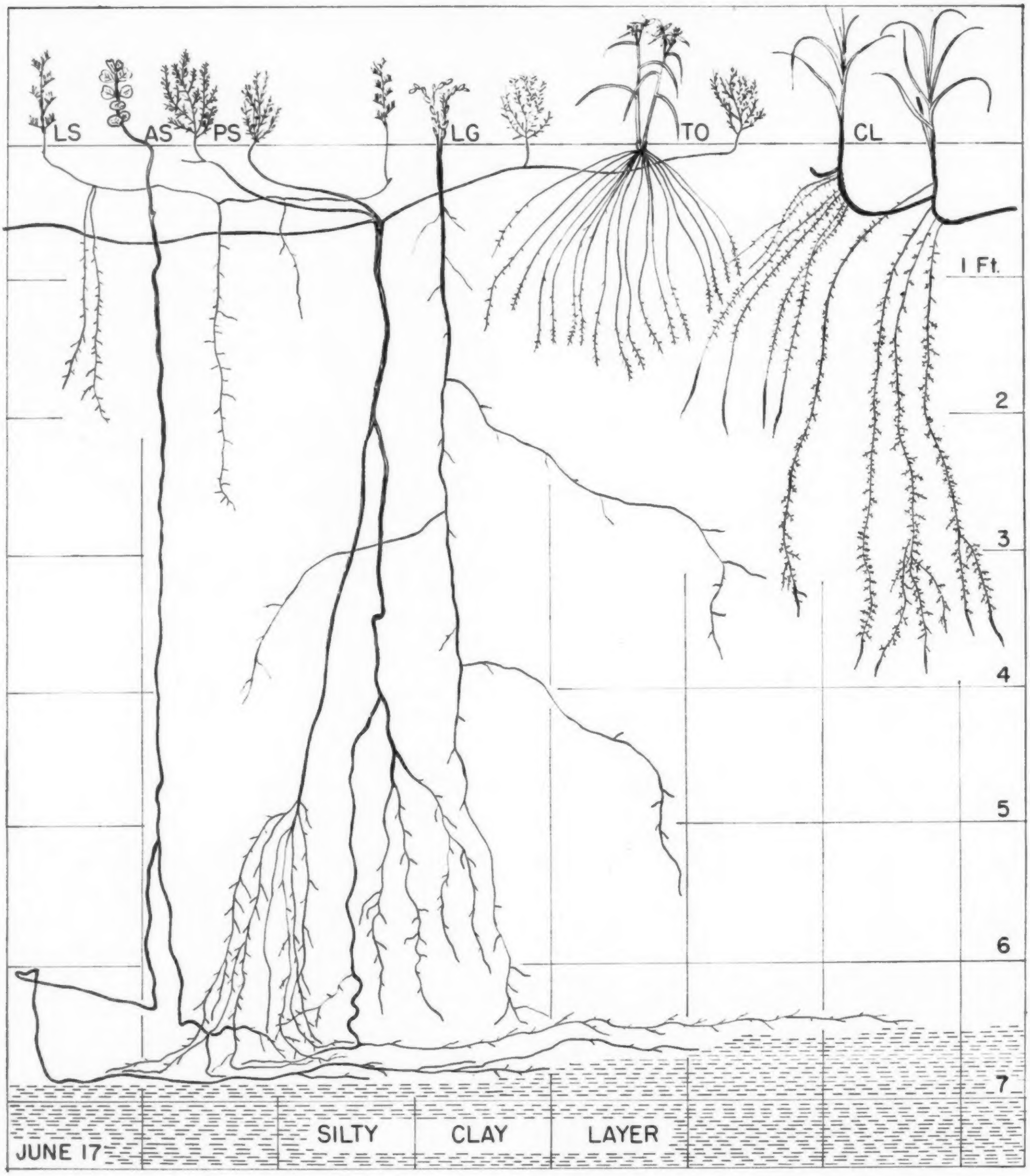

FIG. 24. Bisect showing general form of root systems of several typical sand-dune forbs and grasses growing in sand. *Lathyrus stipulaceus* (LS), *Asclepias arenaria* (AS), *Psoralea lanceolata* (PS), *Lithospermum gmelini* (LG), *Tradescantia occidentalis* (TO), and *Calamovilfa longifolia* (CL).

quadrat, and the sand reedgrass-blue grama community only 3. The number of species of forbs was four times as great as that of grasses, but the basal area of forbs composed only 15.6 percent of the total cover.

The forb populations increased when the dominant grasses were disturbed by grazing or other denuding agents. Communities which were subjected to disturbances over a long period of time had numerous perennial forbs and shrubs, but there were many annual forbs in areas which were disturbed for only a short time.

The forbs and shrubs varied greatly as to their ecological habits and characteristics. Certain species were distinctly pioneers which could not withstand competition. Some were able to endure competition

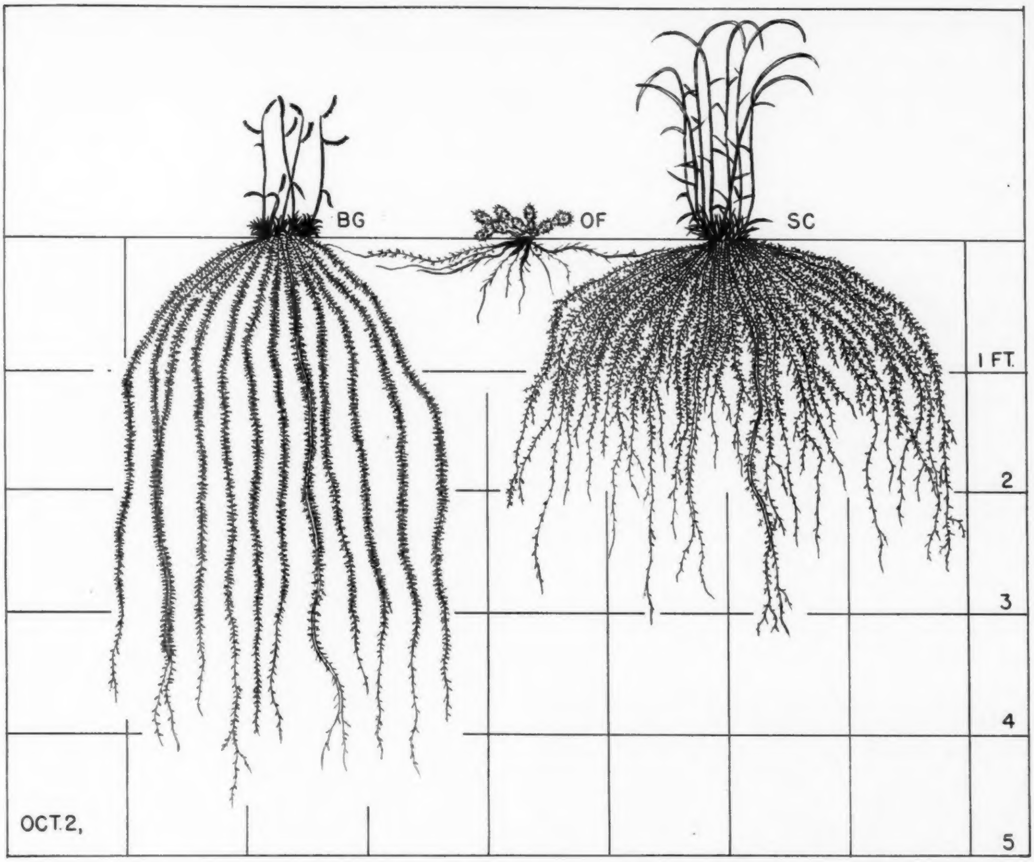

FIG. 25. Bisect showing characteristic root habit of sand dropseed (SC), blue grama (BG), and *Opuntia fragilis* (OF) in the sand dropseed—blue grama community.

with the dune grasses, and others were drought evaders which matured in spring and soon died. Thus the forbs may be placed in various groups.

The five major perennial forbs are spiderwort *(Tradescantia occidentalis)*, skeleton weed *(Lygodesmia juncea)*, prairie sage, perennial ragweed, and sand psoralea *(Psoralea lanceolata)*. Spiderwort frequently grows where competition with the dune grasses is severe, but its growth is aided by disturbance. It is readily grazed by cattle during spring and therefore does not occur abundantly on range lands, but is common in upland pastures used primarily for winter range and for hay making. It flowers in June, seeds immediately, and becomes dormant during the first summer drought. It renews growth in the fall, however, if moisture is present. Migration is by seed only. The succulent roots, which are about 2 mm. in diameter, have only a few laterals and penetrate into the sand 16 to 20 inches (Fig. 24). Spiderwort may be classified as a drought evader.

Skeleton weed is characterized by long slender stems and branches which have leaves only in a rudimentary form. It propagates by long rhizomes. Some flowering heads develop after summer rains, but few seeds mature. Skeleton weed grows on both the sand dunes and the hardlands. Since the stems are grazed by cattle, few plants are found in overgrazed pastures.

Sand psoralea forms socies on dunes and in dry meadows in well developed vegetation, but it makes its best growth as a pioneer in blowouts or in other disturbed places. It spreads by rhizomes from a central root which penetrates to a depth of 8 to 10 feet (Fig. 24). The leaves and pods have an offensive odor and are not readily grazed. The plants remain green throughout the summer in blowouts where they do not compete with grasses, but in mature communities this legume produced no seed and dried soon after the first drought.

Both perennial ragweed and prairie sage spread by rhizomes and thus form large socies. Their root systems are shallow and, therefore, the plants must withstand long summer drought. On receiving moisture, however, they quickly revive. The ragweed is less palatable than the sage and therefore persists

under heavy grazing. Both flower in late summer or fall.

A group of unpalatable, perennial forbs grow where the grasses have been weakened or destroyed by grazing and are thus valuable as indicators of disturbance. Riddell's groundsel (*Senecio riddellii* T. & G.) is a poisonous weed bearing yellow flowering heads in September at the top of stiff stems with narrowly pinnate, succulent leaves. A taproot penetrates 4 to 5 feet beneath the surface.

The bush morning glory (*Ipomoea leptophylla* Torr.) attains a height of 2 to 3 feet; the stems spread 3 to 4 feet laterally from a central crown. The plant is characterized by a fleshy, deep taproot in which water accumulates during periods of rain. Purple flowers appear in the middle of July.

Solitary plants of sand stoneseed (*Lithospermum gmelini* (Michx.) Hitchc.) are scattered throughout the dune habitats. Orange flowers appear in early June. The black taproot penetrates to a depth of 6 to 7 feet (Fig. 24).

The Platte thistle (*Cirsium plattensis*) has a taproot which penetrates to a depth of 3 to 4 feet (Fig. 26). Cream-colored heads appear late in May or early in June.

Certain pioneer plants are unable to withstand competition with the xerophytic grasses. Chief among these are *Rumex venosus, Pentstemon haydeni, Oenothera albicaulis, Phaca longifolia, Comandra pallida, Petalostemon villosus, Oenothera nuttallii* Sweet, and *Machaeranthera canescens* (Pursh) A. Gray. All but Pentstemon, Petalostemon and Machaeranthera are stoloniferous.

FIG. 26. Platte thistle *(Cirsium plattensis)* and leaves of sand-hill bluestem *(Andropogon hallii)* on the side of dune in early June.

A third group, including *Equisetum kansanum, Physalis heterophylla* Nees., *P. virginiana* Mill., *Solidago glaberrima,* and *Helianthus rigidus,* has rhizomes, but is of secondary importance. Seldom, if ever, do these species grow in blowouts, but they invade stabilized sands denuded of vegetation, or grow in the most favorable dune environments. They are true-prairie species on the edge of their geographical or ecological range.

Twenty-four perennial species have no rhizomes and therefore are scattered over the dunes as isolated individuals. They are usually late invaders which can withstand competition with the more xerophytic of the dune grasses, but develop best where vegetation is disturbed. They possess deep taproots. The major species in this group are *Lithospermum linearifolium, Ipomoea leptophylla, Artemisia caudata* Michx., *Lithospermum gmelini, Liatris squarrosa, Petalostemon purpureus* (Vent.) Rydb., *P. oligophyllus* (Torr.) Rydb., *Hymenopappus filifolius* Hook., *Oenothera serrulata* Nutt., *Cirsium plattensis, Senecio riddellii, Psoralea digitata* Nutt., *Chrysopsis villosa* (Pursh) Nutt., *Sideranthus spinulosus* (Pursh) Sweet, *Acerates angustifolia* (Nutt.) Dec., *Asclepias arenaria* Torr., and *Kuhnia suaveolens* Fresen.

A small group of forbs persists in grasslands because of their ability to flower and seed in spring and go into dormancy during the first summer drought. These plants do not readily invade denuded areas but are benefited somewhat by disturbance of the dominant grasses. They occur in a wide range of sandy habitats. Chief among them is *Tradescantia occidentalis,* but plants of similar habit listed in order of importance are *Lathyrus stipulaceus* (Pursh) Butters and St. John, *Pentstemon angustifolius* Pursh, *Lesquerella ludoviciana* (Nutt.) S. Wats., *Senecio plattensis* Nutt., and *Towsendia* sp.

A total of 12 annual forbs and 2 annual grasses grow on disturbed dune sands where competition with the dune grasses is not great. The most common forbs are sand-hill sunflower *(Helianthus petiolaris),* sand spurge (*Euphorbia petaloidea* Engelm.), and narrow-leaved lambsquarter (*Chenopodium leptophyllum* Nutt.). The following annual plants are unable to withstand competition with dune grasses and therefore are present, but in small numbers only, in the most severely disturbed areas. Two chief annual grasses on dune sands are *Triplasis purpurea* (Walt.) Chapm. and *Cenchrus pauciflorus* Benth. The forbs include *Froelichia campestris* Small, *Euphorbia serpens* H. B. K., *Cristatella jamesii* T. & G., *Cycloma artriplicifolium* (Spreng) Coult., *Salsola pestifer, Corispermum villosum* Rydb., and *Lygodesmia rostrata* A. Gray.

Three biennial plants in sand-hill habitats are *Eriogonum annuum, Oenothera rhombipetala* Nutt.,

and *Hymenopappus tenuifolius* Pursh. They are unable to compete with the perennial grasses and therefore indicate disturbances.

Shrubs, listed in order of their importance, include soapweed (*Yucca glauca* Nutt.), sand cherry (*Prunus besseyi* Bailey), poison ivy (*Toxicodendron radicans* (L.) Kuntze), prairie rose (*Rosa arkansana* Porter), Macoun's rose (*R. macounii* Greene), and small redroot (*Ceanothus ovatus* Desf.). They grow best on protected hillsides or in areas where grass cover is reduced by grazing, but occur in small quantities throughout all dune habitats. Sand cherry, prairie rose, and poison ivy have rhizomes, and the roots penetrate to a depth of 8 and 12 feet (Fig. 27).

FIG. 27. A typical view of a sand-hill community in which sand-hill bluestem *(Andropogon hallii)* and sand reedgrass *(Calamovilfa longifolia)* grow above bunches of hairy grama *(Bouteloua hirsuta)*.

Sand cherry flowers early in May, and the others early in June. Fruits develop only during favorable seasons.

Soapweed is conspicuous on heavily grazed ranges and on rough, stony lands. It is seldom found where vegetation is well stabilized. Its stiff, long leaves remain green throughout the winter. The pods appear shortly after flowering and are eaten by cattle. According to the ranchers, the crowns of soapweed are often grazed during the winter, but the plants are not disturbed in the summer when there is an abundance of green forage. Soapweed increased under heavy grazing.

GENERAL RELATIONS OF THE FLORA

The highly diversified and well developed vegetation of the dunes points to a great age and an early historical development of the sand-hill flora. Geological evidence reveals that sand habitats have existed in this region since early Tertiary times. Generic composition of the dune vegetation and the true prairie is similar. The dominant grasses and many of the major forbs of the two communities, however, are distinctly different in species, and some genera are entirely characteristic of sandy habitats. This indicates that the development of dune vegetation was independent of that of true prairie but contemporaneous with it.

Five dominant genera, including Muhlenbergia, Bouteloua, Andropogon, Eragrostis, and Sporobolus, are represented in the flora of the true prairie and the sand hills. Three of these (Andropogon, Sporobolus and Bouteloua) have species which are dominant in the true prairie. Muhlenbergia and Eragrostis are important in the sand-hill flora, but species of these genera are usually disclimax in the true prairie. Only three true-prairie grasses occur on the dunes. *Stipa spartea* is found occasionally; June grass and little bluestem grow only in the most favorable places.

Two genera, each with a single species, are confined to dune habitats. Of these Calamovilfa is the most characteristic of the sand-hill flora and Redfieldia is the most important pioneer in blowouts. Among the forbs there is no genus which occurs only on the dunes, but 52 percent of the species are confined to sandy habitats. Generic relations to the mixed prairie in Nebraska are found only in Bouteloua, but the ecological ranges of the several dune and mixed-prairie dominants overlap, causing mixtures along a broad zone of contact.

Physiologically, the sand-hill grasses are adapted to a mixed-prairie climate under which they withstand severe aerial environment and endure long periods without rain. As a result of efficient absorption of summer rains, more moisture is available to the individual plant in the sand hills than on the hardlands. Wide spacing of plants and ability of certain species (including the tall grasses) to penetrate several feet into the sand are adaptations to the habitat. They are, however, unable to withstand competition of the mesophytic tall grasses in the meadows. Conversely, they are too mesic to endure competition with the climax grasses on the hardlands.

LAYERING

Two grasses are usually dominant in dune communities, and several grasses and forbs occupy a position of secondary importance (Fig. 27). One dominant is usually a tall grass and another a short bunch grass. The major tall grasses are *Calamovilfa longifolia* and *Andropogon hallii.* To this group *Redfieldia flexuosa* may be added, though it grows

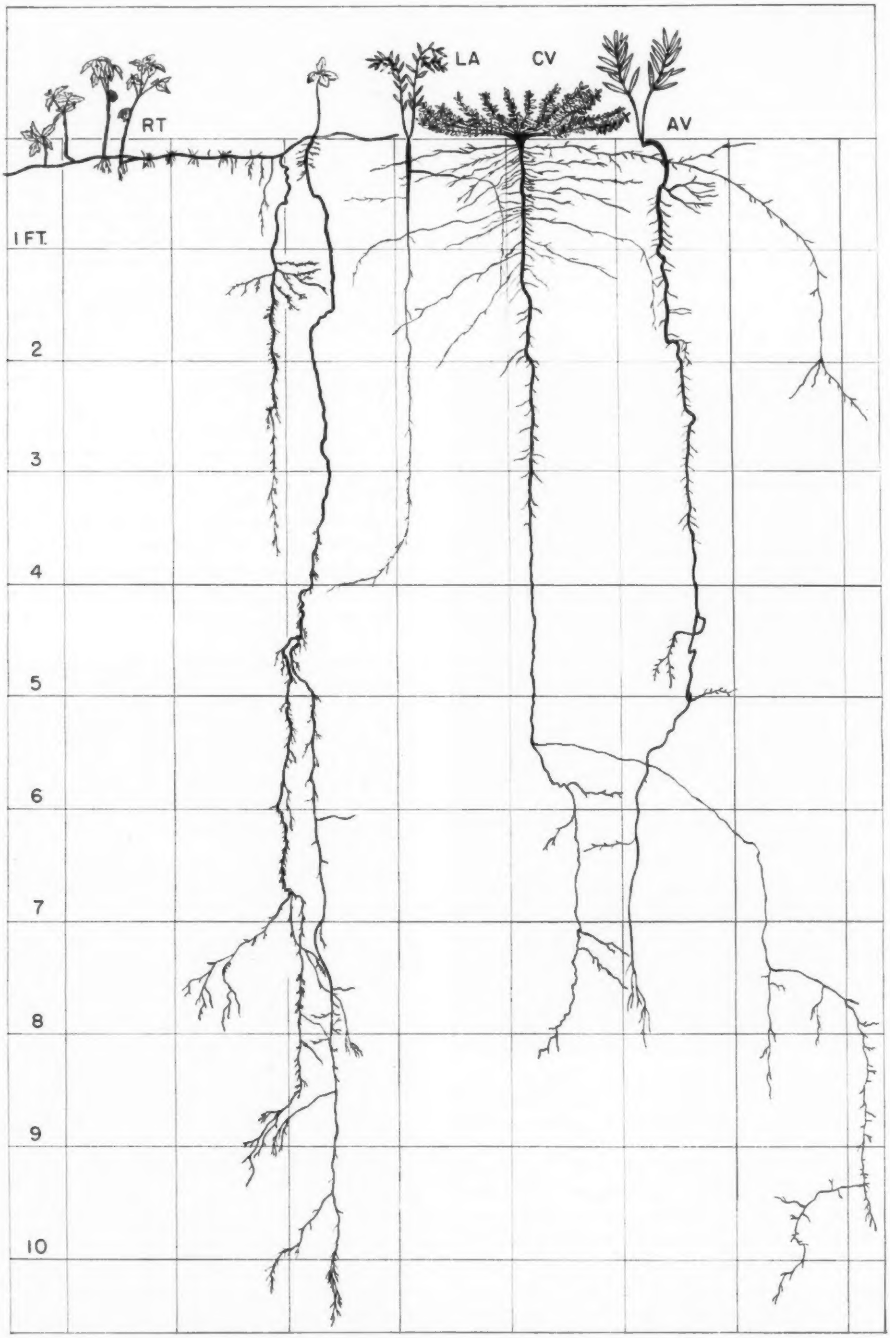

FIG. 28. Bisect showing root systems of several typical sand-dune forbs and shrubs. Poison ivy *(Toxicodendron radicans)* (RT), narrow-leaved puccoon *(Lithospermum linearifolium)* (LA), *Chrysopsis villosa* (CV), and *Acerates* sp. (AV).

only occasionally in a mixed community. Sand-hill muhley, though shorter in stature, is an ecological equivalent of the tall dune grasses. The typical tall dune grasses form a layer 2 to 4 feet above a lower stratum which is composed primarily of hairy grama, sand dropseed, sand-hill sedge, blue grama, western needlegrass, and many of the forbs. The true-prairie bunch grasses—little bluestem and June grass—are not only of secondary importance, but also attain a height only slightly greater than the short bunch grasses.

The short-grass layer is poorly developed in the Eragrostis community on the dunes. The tall-grass layer is absent only in the sand-hill muhley-hairy grama community on the tops of the dunes, where sand-hill muhley occupies the ecological position of a tall grass. It has a root growth similar to the tall grasses and is more mesophytic than its bunch-grass codominant. Absence of the ground layer in the Eragrostis community is the result of inability of the short grasses to withstand shading by the tall grasses and competition for moisture with a larger grass of similar root habits.

Layering is clearly evident beneath the soil surface just as it is above. There are two layers above ground and two below. A group of xerophytic bunch grasses are rooted only 12 to 18 inches deep, and are dependent upon summer rain for most of their water. Their fine roots thoroughly ramify the surface sands, and the plants transpire all available water soon after a rain. Hence, they must endure long periods of drought. *Eragrostis trichodes* is the largest bunch grass in the dunes. It is confined to the most favorable habitats on north-facing slopes. Sand dropseed and hairy grama are similar to Eragrostis in structure, but differ in size. Sand dropseed, a mid-grass, is most common where the climax grasses are disturbed. Hairy grama, the shortest of the three, is the most abundant on top of the wind-swept dunes and in the ground layer of the sand reedgrass and sand-hill bluestem communities.

The tall grasses with widely spaced stems and rhizomes have deep, well spaced roots. They absorb some moisture in the surface sands where they compete with the short, shallow-rooted bunch grasses, but in addition their roots penetrate 4 to 10 feet in depth and absorb water slowly throughout the growing season. This source of water is a valuable supplement to summer rain, especially during long periods of drought. It is largely for this reason that the tall grasses and many of the shrubs and forbs are able to survive in a region of prolonged summer drought. Redfieldia and Muhlenbergia have roots similar to the tall grasses, but they do not penetrate as deeply, nor do the plants occur where competition with the shallow-rooted bunch grasses is great.

Many successful forbs and small shrubs have root systems similar to the tall grasses in that they penetrate deeply into the sand (Figs. 5, 20, 24, and 27). The chief forbs are *Psoralea lanceolata, P. digitata, Asclepias arenaria, Petalostemon villosus, Oenothera serrulata, Apocynum cordigerum, Lithospermum gmelini,* and *Sideranthus spinulosus.* All the small shrubs including soapweed, prairie rose, sand cherry, and poison ivy have roots which penetrate 10 to 12 feet deep.

The shallow-rooted forbs are either confined to mesophytic habitats, or they are drought enduring or drought escaping (cf. Shantz 1927). Prairie goldenrod, upland sunflower, and perennial ragweed are confined to the favorable dune habitats. Prairie sage and cacti endure long periods of drought, but the early flowering *Lathyrus stipulaceus, Rumex venosus, Tradescantia occidentalis, Pentstemon angustifolius,* and *Lesquerella ludoviciana* are drought escaping.

BASAL COVER

Plant stems and bunches are widely spaced in sand-hill communities. Basal cover varied from 1 to 3 percent (Table 3). Grasses comprised 85 percent of this cover. Bunch grasses are the most important. For this reason the sand-hill muhley-hairy grama community had a basal cover of 2.7 percent. There was a similar density in the tall-grass communities where blue or hairy grama were present, as in the sand-hill bluestem community (2.2 percent) and the sand reedgrass-blue grama community (1.9 percent). In a pure stand of sand reedgrass, basal cover was only 1 percent.

Blowout grass, sand-hill muhley, sand reedgrass, sand-hill bluestem, and sand-hill sedge have rhizomes 4 to 8 inches in length. Sand dropseed, with rhizomes 2 to 3.5 inches long, grows in open bunches. Sand-hill lovegrass and hairy grama are the only important grasses which grow in dense bunches, and June grass and little bluestem also have this habit of growth. The bunches are widely spaced, and the stems of the rhizome-bearing species are evenly distributed throughout the communities. Among 34 common forbs, 28 species have rhizomes.

SEASONAL ASPECTS

Species contributing to the prevernal aspect are few, and they are not numerous on the dunes. Sand-hill sedge flowers in middle April. *Lathyrus stipulaceus, Prunus besseyi,* and *Rumex venosus* are the first plants to unfold conspicuous flowers. They usually appear in early May.

The vernal aspect from middle May to late June is characterized by moderate temperatures and conditions favorable to plant growth. Forbs do not normally grow in sufficient quantity to give color to the landscape dominated by the greens and grays of living and dead grass, but spiderwort and yucca are occasionally conspicuous in disturbed grassland. Western needlegrass, Indian ricegrass, and June grass flower during this period. Most conspicuous among the forbs which flower at this time are *Lesquerella ludoviciana, Lithospermum gmelini, Pentstemon angustifolius,* and *Tradescantia occidentalis* (Fig. 29).

The estival season begins about June 15 and continues until late July. It is characterized by period-

TABLE 3. A summary of grasses of 25 census and basal area quadrats from each of eight stations from several, typical, well-developed plant communities on Fort Niobrara Game Preserve. It illustrates differences in composition according to variation in soil texture and topography.

	Communities of dune sands										Communities of mixed prairie			
	Muhlenbergia pungens—Bouteloua hirsuta		*Andropogon hallii—Bouteloua hirsuta*		*Eragrostis trichodes—Calamovilfa longifolia*		*Calamovilfa longifolia*		*Calamovilfa longifolia—Bouteloua gracilis*		*Sporobolus cryptandrus—Bouteloua gracilis*		*Stipa comata—Carex filifolia*	
Hygroscopic coefficient.......	0.7		0.8		0.9		1.3		1.0		2.0		4.5	
Topography.....	Top of steep dune		Upper break of steep dune		North-facing dune		South-facing dune		Level area in a dry valley		Level land		Level land	
Criteria.........	Stem counts*	Basal area	Stem counts	Basal area	Stem counts	Basal area	Stem counts	Basal area	Stem counts	Basal area	Stem counts	Basal area	Stem counts	Basal area
Agropyron smithii.....	......	......	......	......	......	......	......	......	......	......	......	......	...241	222
Carex filifolia.........	......	......	......	......	......	......	......	......	......	......	(57)	569	(2,950)	5,371
Stipa comata.........	......	......	(7)	18	(18)	32	(16)	70	(61)	78	(114)	639	(527)	5,033
Bouteloua gracilis......	......	......	(31)	212	......	......	......	......	(472)	2,955	(583)	5,654	(981)	3,265
Sporobolus cryptandrus.	144	137	254	247	195	178	417	359	307	270	3,196	3,171	69	69
Calamovilfa longifolia ..	361	161	335	169	479	265	3,421	1,540	2,545	1,154	183	87	30	30
Carex heliophila.......	16	13	407	353	92	79	433	355	203	156	1	4	14	18
Andropogon hallii......	75	65	1,171	1,084	64	51	53	43	196	147	18	14	......	......
Bouteloua hirsuta......	(335)	2,361	(321)	2,219	......	......	(3)	3	(27)	129	(10)	114	......	......
Andropogon scoparius..	(47)	842	(170)	805	(7)	16	(3)	20	(1)	1	......	......	......	......
Koeleria cristata.......	(3)	95	(28)	202	(4)	8	......	......	(1)	1	......	......	......	......
Eragrostis trichodes.....	......	......	......	......	(178)	4,330	(36)	279	......	......	......	......	......	......
Muhlenbergia pungens..	4,577	2,806	99	99	......	......	......	......	......	......	......	......	......	......
Redfieldia flexuosa.....	19	7	......	......	107	45	1	1	......	......	......	......	......	......
Cyperus schweinitzii....	20	16	4	2	1	1	......	......	......	......	......	......	......	......
Aristida longiseta......	(11)	230	......	......	......	......	......	......	......	......	......	......	......	......
Total basal area.......	......	6,733	......	5,410	......	5,005	......	2,670	......	4,893	......	10,252	......	14,028
Percent of basal area ..	......	2.7	......	2.2	......	1.9	......	1.0	......	1.9	......	4.1	......	5.6

*Numbers in parenthesis indicate number of bunches.

FIG. 29. Sand puccoon *(Lithospermum gmelini)* in flower during early June.

ical drought. During the early summer, June grass and needlegrass ripen seed, and sand dropseed, blue grama, and western wheatgrass bear flowers if moisture is sufficient. Most of the sand-hill dominants also bloom when rain occurs. After a heavy rain, flowers of many forbs appear. Most important of these are *Oenothera serrulata, Sideranthus spinulosus, Argemone intermedia, Asclepias arenaria, Acerates* sp., *Lygodesmia juncea, Apocynum cordigerum, Ipomoea leptophylla, Liatris squarrosa, Petalostemon oligophyllus, P. purpureus, P. villosus* Nutt., and *Solidago glaberrima.*

The autumnal aspect begins about the first of August. The fall is characterized by rapid shortening of the days and lowering temperatures. The occurrence of timely showers make this a period favorable to plant growth. Though the sand-hill grasses may flower sparingly during the estival season, drought commonly delays anthesis until this period. The most important fall-blooming forbs belong to the Compositae. They are *Chrysopsis villosa, Artemisia gnaphalodes, A. caudata, Aster oblongifolius, Machaeranthera canescens, Senecio riddellii, Kuhnia suaveolens,* and *Ambrosia coronopifolia.*

MIXED PRAIRIE

Mixed prairie occurs on the sandy loams and in transitional zones with Valentine sands where hygroscopic coefficients vary from 2.5 to 4.5 percent.

These soil textures determine the disposal of rain and cause conditions to which the mixed-prairie grasses are most adaptable. There is no runoff on the flat and sandy areas, and moisture penetrates to 5 feet in depth in the fine sandy loam soils. Soil texture and its relation to absorption of rain has more effect upon composition of the mixed prairie than do differences in the aerial environment. The zone of transition between mixed-prairie and dune communities is broad. The presence of Calamovilfa in sufficient quantities to be of primary importance marks the transition of the mixed-prairie with the tall-grass communities on the dunes.

SUCCESSION AND DEGENERATION

Stages in development of the mixed prairie in abandoned fields on the hardlands illustrate the course of succession. Such fields are first occupied by annuals, chiefly *Salsola pestifer*, *Amaranthus retroflexus* L., *Setaria viridis* (L.) Beauv., *Chenopodium album* L., and *Panicum capillare*. The most important grasses among the early invaders are sand dropseed and western wheatgrass. Wheatgrass is more successful because it propagates by rhizomes. Once a few seedlings are established, increase is so rapid that in a few years wheatgrass occurs in almost pure stands. In the final stages of succession, the short grasses and western needlegrass enter, and western wheatgrass is eventually reduced to a position of minor importance.

Stages in degeneration of pastures in the mixed prairie are shown in Table 4. Needlegrass and niggerwool form the climax community. Three stages in degeneration follow. Under moderate grazing the quantity of needlegrass is reduced, but the growth of niggerwool and blue grama increases. In the second stage of degeneration blue grama becomes completely dominant, and niggerwool disappears. In the final communities under heavy grazing, very open stands of blue grama and an occasional colony of buffalo grass (*Buchloe dactyloides* (Nutt.) Engelm.) occur between large patches of unpalatable perennial and annual forbs.

TABLE 4. The total number of bunches (numbers in parenthesis) or stems of grasses in 25 census and basal area quadrats from each of four mixed-prairie communities. Differences in composition and basal cover resulting from grazing and drouth are shown. The first community is climax, and the others represent successive degrees of degeneration.

Plant community →	Needlegrass—niggerwool		Blue grama—niggerwool Station A		Blue grama—niggerwool Station B		Blue grama	
Species	Stems or bunches	Basal cover sq. cm.	Stems or bunches	Basal cover sq. cm.	Stems or bunches	Basal cover sq. cm.	Stems or bunches	Basal cover sq. cm.
Agropyron smithii	241	222	14	11	......	......	......	.....
Carex heliophila	12	18	1	1	......	......	......	.....
Buchloe dactyloides	......	......	......	......	......	......	(71)	193
Stipa comata	(527)	5,053	(138)	739	28	67	......	.....
Carex filifolia	(2950)	5,371	(3287)	7,051	(1012)	1,240	......	.....
Bouteloua gracilis	(981)	3,265	(2025)	12,782	(1640)	8,229	(1773)	7,489
Sporobolus cryptandrus	69	69	3	10	102	99	......	.....
Total basal cover	......	13,998	......	20,584	......	9,635	......	7,682

FIG. 30. Western wheatgrass *(Agropyron smithii)* in lowlands on fine sandy loam soils.

Agropyron smithii.—Western wheatgrass as a postclimax species occupies ravines and areas which receive run-in water (Fig. 30). As a disclimax grass it occupies uplands where the climax grasses have been destroyed by plowing or other disturbances. It invades bare areas rapidly by means of rhizomes, but usually does not mature a crop of seed under the climate of mixed prairie. In the uplands it is unable to compete with blue grama and needlegrass, but in lowlands it attains sufficient height and density to exclude the short grasses.

Western wheatgrass begins development in the middle of April. When moisture is plentiful, it attains a height of 24 to 30 inches by the first of July, but in dry years it is only 6 to 8 inches tall. It becomes semidormant during periods of drought in summer, but renews growth with advent of autumnal rains. An excellent growth was attained in 1938 when nearly 30 percent of the culms bore flowering heads. A dozen quadrats on an area of Brule

clay yielded an average of 1,848 stems, and a similar number of quadrats in a slightly saline meadow in a sand-hill valley had 1,266 stems. Basal cover was 6.1 and 4.2 percent respectively; foliage cover was nearly 100 percent.

Buchloe dactyloides.—Buffalo grass grows neither on the sand dunes nor in the dry meadows but is confined to the hardlands. On the fine sandy loam soils it is present only in the severely grazed pastures where the climax grasses are destroyed. It is also a disclimax species in the broad ravines in the hardlands where western wheatgrass is dominant in fully developed vegetation. On a few areas of Brule clay in the Niobrara Valley and on local areas of Rosebud silt loam soil on the Crookston Table, buffalo grass is an important part of the mixed prairie.

Buffalo grass grows in small bunches which are well spaced as the result of propagation by runners. On the prairie, it seldom attains a height of more than 4 inches. Flowers appear earlier than those of blue grama and usually during the first half of June.

Bouteloua gracilis.—Blue grama is the chief disclimax species in the mixed prairie (Fig. 31). It

FIG. 31. Blue grama *(Bouteloua gracilis)* with small quantities of sand dropseed *(Sporobolus cryptandrus)*. Herbaceous plants in the foreground are prairie sage *(Artemisia gnaphalodes)*.

forms nearly pure stands under heavy grazing, but occurs only in small quantities with Calamovilfa in the broad, dry valleys in the sand hills, and in the climax needlegrass community on the hardlands. It grows as a codominant with sand dropseed where dune sands have been deposited in a thin layer over fine sandy loams. Here the hygroscopic coefficients of the surface sands are 2 to 3 percent, and that of the loamy materials 6 to 18 inches beneath the surface are 4 to 5 percent. In such soils the efficiency of absorption of rainfall by dune sand is combined with high moisture holding capacity of the fine sandy loam.

In this transition zone, sand dropseed and blue grama form climax communities. In an area where the surface sands had a hygroscopic coefficient of 2 percent, blue grama was first, sand dropseed second, and needlegrass third in amount of basal cover. In a more silty sand with a hygroscopic coefficient of 2.5 percent, blue grama again ranked highest in amount of basal cover, but needlegrass was second, and sand dropseed, third. The number of bunches of needlegrass and blue grama was 60 and 165 percent higher, respectively, in the more silty sand than at the sandier station, but stems of sand dropseed decreased 17 percent.

Blue grama forms low, dense bunches or sods usually 1 to 3 inches in diameter but sometimes 8 to 12 inches. The culms are 12 to 14 inches tall when moisture is plentiful, but usually do not exceed 8 inches during dry years. An average of 4 green leaves with blades 1 to 2 inches in length develop on each culm.

Growth begins late in April or early in May, and the flowering period extends from the last week of June until September, according to the occurrence of rain. Seed production is often light, and for this reason blue grama does not have the pioneer character of sand dropseed. Initiation of root growth from rhizomes occurs during the last two weeks in May. By August the number of roots on each new rhizome ranged from two to six; the average number was three. Mature roots are 4 to 5 feet in length (Fig. 25).

Carex filifolia.—Niggerwool grows in small bunches with needlegrass in climax communities on the hardlands. It is the major species in the ground layer where it attains a height of 3 to 5 inches. In moderately grazed pastures where there are small quantities of needlegrass, growth of niggerwool is increased. Under heavy grazing, however, it is destroyed (Table 4).

Growth begins early in April, flowering occurs late in the month and seeds are usually ripe by the first week in June. The plant becomes dormant in summer but renews growth in autumn when moisture is present. The black roots, which penetrate to a depth of 2 to 3 feet, are stiff, supposedly from large silicous accumulations (Fig. 32). They remain in the soil many years after the plants have died.

Stipa comata.—Western needlegrass grows on hardlands and in the sand hills where soil texture varied from fine sand to fine sandy loam (Fig. 33). It is dominant, however, only on the fine sandy loam soils where hygroscopic coefficients average 4.5 percent. Bunches of needlegrass in the climax community averaged 9 sq. cm. in basal cover. Twenty-one bunches were present in an average quadrat. At a station on Valentine fine sand, the single bunch averaged 9 sq. cm., and an average of 25 bunches were present per quadrat. Like niggerwool, it begins growth in the prevernal season before the short grasses and thus becomes a successful competitor for soil moisture. It attains sufficient height to shade the short grasses in periods of good rainfall. Its leaves remain curled during summer and fall drought, but upon occurrence of rain quickly revive. Three leaves with blades 12 to 14 inches in length were on each culm. The height of culms averaged 26 to 32

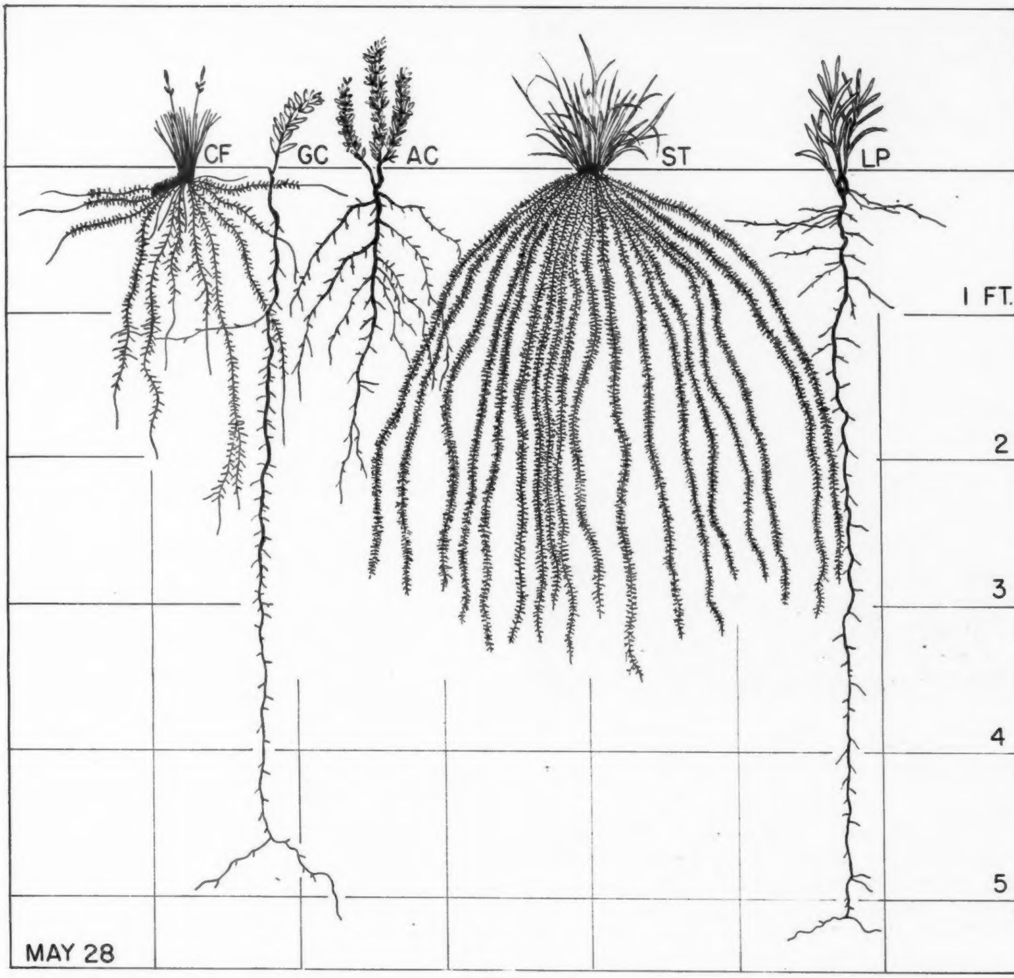

FIG. 32. Bisect in a mixed prairie community on fine sandy loams on the Crookston Table showing root systems of several characteristic grasses and forbs. Niggerwool *(Carex filifolia)* (CF), *Gaura coccinea* (GC), *Artemisia caudata* (AC), western needlegrass *(Stipa comata)* (ST), and *Liatris punctata* (LP).

inches. Few plants had mature seed or yielded much forage without the benefit of early summer rains. In 1936, 1937, and 1939 few seeds formed, but in 1938 a full crop matured. The roots penetrated to a depth of 3 feet (Fig. 32).

The grasses of secondary importance usually occur in disturbed vegetation or they are pioneers on abandoned fields. They are western wheatgrass, sand dropseed, buffalo grass, sand reedgrass, green needlegrass (*Stipa viridula* Trin.), tumblegrass (*Schedonnardus paniculatus* (Nutt.) Trelease), and red three-awn grass (*Aristida longiseta* Steud.).

FORBS OF MIXED PRAIRIE

Most perennial forbs of the mixed prairie increase under moderate disturbance caused by grazing. They are most common in areas which receive runoff water. The most important are: *Pentstemon albidus* Nutt., *P. grandiflorus* Nutt., *Kuhnia suaveolens, Echinacea pallida* (Nutt.) Britton, *Liatris punctata* Hook., *Artemisia gnaphalodes, Psoralea argophylla, Oenothera nuttallii, Solidago mollis* Bartl., *S. glaberrima, Aster ericoides* L., and *Sideranthus spinulosus.*

Cacti or prickly pear and certain unpalatable perennial forbs and shrubs grow in heavily grazed pastures, where needlegrass and niggerwool have been destroyed and blue grama materially reduced by grazing. They are *Opuntia fragilis* (Nutt.) Haw., *O. humifusa* Raf., *Artemisia caudata*, and *A. frigida* Willd.

Winter annuals are found in disturbed vegetation, especially in communities of blue grama. Sometimes the seeds germinate in the fall and pass the winter in the seedling stage. Often they remain in the soil

FIG. 33. Western needlegrass *(Stipa comata)* with niggerwool *(Carex filifolia)* in a climax community of the mixed prairie undisturbed by grazing.

for several seasons until the environment is favorable to their germination. Winter annuals flower in the spring and early summer. Seed matures about the time hot weather begins. The chief species are *Bromus japonicus* Thumb., *Festuca octoflora* Walt., *Lepidium densiflorum* Schrad., *Plantago purshii* R. & S., and *Lappula occidentalis* (S. Wats.) Greene.

Two biennial species, *Oenothera rhombipetala* Nutt. and *Hymenopappus tenuifolius* Pursh, are confined to very fine sandy soils. *Yucca glauca, Artemisia frigida, Amorpha canescens,* and *Rosa arkansana* likewise grow on these soils, but are also present in disturbed phases of vegetation on fine sandy loams and occur in areas which receive run-in water.

LAYERING

Well developed communities are characterized by two layers above ground. A group of mid grasses, including needlegrass, western wheatgrass, and sand dropseed, form a layer 18 to 24 inches above a lower one which is composed of blue grama and niggerwool. Several species of forbs are found in both layers.

Root layering is not as obvious in the mixed prairie as in the dune communities, since moisture does not penetrate beyond 4 to 5 feet. There is, however, a concentration of roots near the surface. The root systems of blue grama, needlegrass, and niggerwool penetrate to a depth of 3 to 4 feet (Fig. 32). Forbs have taproots which approximate the same depth. Roots of cacti are shallow (Fig. 25).

SEASONAL ASPECTS

The greatest growth in mixed prairie was made in spring. Summer rains are too light and infrequent to supply moisture in sufficient quantity to sustain much growth. Inefficient absorption by the soil also causes much loss of water by runoff. Autumn is usually a period of revival.

Flowering in the mixed prairie occurred mainly in spring and autumn. The time of revival in spring is important in survival and dominance. The grasses which begin growth in the prevernal season and flower before the drought are the climax species. Those which are slow to renew growth and flower in early summer or midsummer are mostly disclimax species.

Needlegrass and niggerwool are effective competitors for moisture because they begin growth early in spring and mature seed prior to the occurrence of prolonged drought. Western wheatgrass, the dominant in lowlands, also begins growth during the prevernal season, but may not flower until July. It seldoms bears a crop of seed. This type of reproduction, however, is of little importance to western wheatgrass because it propagates extensively by long rhizomes. Blue grama renews growth later than the other climax species, but it flowers at about the same time as western wheatgrass. Buffalo grass renews growth in spring at the same time as blue grama, but it flowers in early June. Time of anthesis, however, depends upon occurrence of rain. Blue grama may flower as late as the middle of September.

In the vernal aspect the most conspicuous flowers are those of *Malvastrum coccineum, Gaura coccinea, Pentstemon grandiflorus, P. albidus,* and *Cheirinia aspera.* Those which bloom in the late summer and fall are *Liatris punctata, Aster ericoides, Artemisia caudata,* and *A. frigida.*

BASAL COVER

The climax community on the hardlands had somewhat higher basal cover (5 percent) than those of the sand hills. Moderately grazed pastures, where blue grama and niggerwool were dominant, had a basal cover of 8 percent. This was a reaction of the short species to a decrease in competition with needlegrass. In severely grazed areas, however, basal cover was considerably less. At a station which was dominated by blue grama but which had a few plants of niggerwool, the basal cover averaged 3.4 percent; in a poor stand of blue grama, the basal cover was 3.0 percent.

WOODLAND

There are approximately 10,000 acres of woodland in Cherry County. Trees, shrubs, and a relic, herbaceous flora meet in postclimax communities in the river valleys. The deciduous trees grow in well

aerated soils where moisture is available from a stable water table throughout the year. Woodlands are common in the deep canyons and immediately along the streams, but the broad river valleys are usually occupied by scattered groves of trees alternating with chaparral and tall-grass meadow. The ecotone between the deciduous woods and the mixed prairie on the hillsides is narrow because of marked changes in depths to the water table. The largest and best developed deciduous woodland is found along the south side of the Niobrara Valley for a distance of 25 miles east of Valentine.

Ponderosa pines grow with other Rocky Mountain plants on rough, stony land where run-in water is received from rock surfaces and where snow lodges during the winter. They are located well above the water table and must withstand varying periods of drought. Seedlings do not become established on broad, gentle slopes because the grasses are better equipped to obtain the available moisture. Shade in the deciduous woodland is too great for their development.

Most of the timber was cut by the early settlers 50 to 60 years ago. Since then the coniferous trees have reproduced from seed, and much second growth of deciduous trees has developed from the stumps. Since fire has been under control, trees have advanced into the chaparral and grasslands as far as the environment permitted. Because deciduous trees are able to grow only where their roots have access to a permanent water table, there was little loss from drought. Ponderosa pine is especially resistant to drought, and only rarely were trees killed. But in a few dry canyons, which did not have a favorable water supply, mortality of the chaparral was as great as 85 to 95 percent.

The deciduous woodland is composed largely of flood-plain species, but a few trees which usually grow on the valley hillsides in the eastern part of Nebraska occupy the more xeric habitats in the flood plain. Sandbar willow (*Salix interior* Rowlee) grows on sands recently deposited along the Niobrara River. Peach-leaved willow (*Salix amygdaloides* Anders.) and Sargent's cottonwood (*Populus sargentii* Dode) are the chief trees on more stabilized river sand. Most of the flood plains and river banks, however, have not been disturbed for a long time. The dominants of the flood plains are the chief species. They include American elm (*Ulmus americana* L.), green ash (*Fraxinus lanceolata* Borkh.), red ash (*Fraxinus pennsylvanica* Marsh.), box elder (*Acer negundo* L.), and hackberry (*Celtis occidentalis* L.) (Fig. 34).

Ironwood (*Ostrya virginiana* (Mill.) K. Koch) and paper birch (*Betula papyrifera* Marsh.) grow about springs on the north-facing hillsides east of Valentine. A small stand of *Populus tremuloides* Michx. was also found in this habitat. Bur oak (*Quercus macrocarpa* Michx.), elm, ash, box elder, and red cedar (*Juniperus virginiana* L.) occur on these slopes where ground water is probably present in only small amounts at certain periods during the summer months.

FIG. 34. View of deciduous woods in Niobrara Valley. The major tree is American elm *(Ulmus americana)*. The grass in the foreground is *Elymus villosus*.

Shrubs grow beneath the trees and along the margins of woodlands, and sometimes form stands several acres in extent in the broad flood plains and on the steep, north slopes of dunes. The chief shrubs are choke cherry (*Prunus melanocarpa* (A. Nels.) Rydb.), buckbrush (*Symphoricarpos occidentalis* Hook.), wild plum, golden currant (*Ribes odoratum* Wendl.), prairie rose, poison ivy, Macoun's rose, and lead plant. Buffalo berry (*Shepherdia argentea* Nutt.) and sumac (*Rhus glabra* L.) occupy similar habitats but are of minor importance.

Shrubs confined to the habitats immediately along river banks and edges of swamps are dogwood (*Cornus interior* Rydb.), black currant (*Ribes americanum* Mill.), blue indigo (*Amorpha fruticosa* L.), and Missouri willow (*Salix missouriensis* Bebb.).

Three species of vines in open woodlands are wild grape (*Vitis vulpina* L.), Virginia creeper (*Parthenocissus quinquefolia* Planch.), and bittersweet (*Celastrus scandens* L.). Bittersweet is a twiner but the other two have tendrils.

Grasses and forbs in the moist woodlands have a foliage cover of nearly 100 percent, except in the most shaded portions and in the driest parts. The vernal aspect is dominated by *Carex sprengelii* Dewey, and that of summer by *Elymus villosus* Muhl. and *E. virginicus* L. Disclimax phases of woodlands are dominated by annual weeds, chief of which are

Chenopodium album, Collomia linearis Nutt., *Lappula virginiana* (L.) Greene, and *Parietaria pennsylvanica* Muhl.

Hackberry forms small groves with only a few to as many as 100 trees in the hollows (old blowouts) on north sides of dunes and in river valleys. The trees on the lower edge of the grove at Hackberry Lake probably have access to the water table 10 to 15 feet beneath the surface. Here they attained a height of 24 to 30 feet. Trees on the upper edge were only 8 to 10 feet high. The ages of these trees, which were determined by the use of an increment borer, ranged from 33 to 45 years and averaged 40 years. Diameters at breast height (D. B. H.) averaged 5 inches. Distances between trees varied from 4 to 10 feet, but two trunks commonly grew together. The crowns of the trees formed nearly a complete cover. Shrubs and herbs grew beneath the hackberry trees where stock was excluded.

Bur oak is at its western limit in the Niobrara Valley 15 to 20 miles west of Valentine. It becomes shrub-like and attains a height of only 15 to 20 feet where moisture is limited. The trunks have a diameter of 2 to 7 inches. Where an abundant supply of ground water was available, the trees were 40 to 50 feet tall. Some of the mature trunks were 21 to 34 inches thick (D. B. H.), and the trees were 200 to 250 years old. Most of them, however, were less than 50 years of age and had a diameter of only 12 to 18 inches.

Red cedar grows in scattered stands throughout the deciduous woodlands and occurs in pure stands locally, especially in the shallow valley near the headwaters of Schlegel Creek. Here it forms a transition zone 2 to 3 miles in length between the deciduous woodlands in a deeper portion of the valley and chaparral in a shallower one. It also grows in pure stands on the upper edge of the deciduous woodlands in a zone of transition to ponderosa pine. The tallest trees were 25 to 30 feet high and 30 to 40 years old.

Ponderosa pine is usually found on rough, stony lands where water runs in from rock surfaces (Fig. 35). Continuous stands of pine grow along the edge of the Crookston Table on exposures of the Ash Hollow limy sandstone formations from Valentine eastward to Springview in Keya Paha County. A growth of pine on the south side of Niobrara Valley east of Valentine and on both sides of the valley from Valentine westward through Sheridan County occurs only in isolated stands. A continuous stand grows on the canyon walls of Schlegel, Gordon, and Snake valleys. Probably all habitats favorable to the growth of pine seedlings are now occupied by established trees, and little opportunity remains for enlargement of stands through natural propagation.

FIG. 35. Ponderosa pine alternating with the mixed prairie on rough, stony land in the Niobrara Valley. The deciduous trees are bur oak.

The average age of 120 trees of ponderosa pine at three stations near Valentine was 44 years. The average height was 25 feet, and the average D. B. H., 8 inches. Certain pines were isolated while others were only a few feet apart. Average distance between trees in two groves was 7 feet. Branches of pine trees 40 to 50 years of age overlapped those of adjacent trees when the trunks were less than 15 feet apart. A tree more than 175 years of age, observed at Fort Niobrara Game Preserve, had a D. B. H. of 33 inches and attained a height of 70 feet. Another tree 24 inches in diameter and 75 feet tall was over 103 years old. Only 17 percent of the trees were under 25 years of age. Little reproduction has taken place during the past 20 years.

Ponderosa pine has been successfully planted on both the hardlands and the sand hills. An excellent example of the growth of pine on dune sands is found in the Nebraska National Forest. A planted grove 30 years old on a hardland area had an average height of 24 feet and a D. B. H. of 7 inches. Growth of red cedar from planted seedlings has also been successful.

The most important shrubs associated with ponderosa pine are white sage, soapweed, fetid sumac (*Rhus trilobata* Nutt.), poison ivy, prairie rose, sand cherry, western choke cherry, and match weed (*Guiterrezia sarothrae* (Pursh) Britton and Rusby).

SUMMARY

The sand-hill region in Nebraska is grassland with a variety of habitats caused by differences in soil and sand textures, drainage, and topography.

The annual average rainfall is 18 inches. High temperature, low humidity, prevailing south wind, and frequent drought are unfavorable to plant growth through a part of the summer. Greatest growth is made in spring and fall.

Sand efficiently absorbs moisture. There is no runoff, and loss by evaporation from the surface is small. Fine sandy loams are less efficient in absorption of rain. Efficiency of absorption is especially important during the critical months of summer and is the major cause for differences in composition of vegetation on the several textures of soil on the uplands. Topography also modifies aerial environment and causes local differences in composition of vegetation, especially in the sand hills.

Sampling of soil for moisture showed that pioneer communities use available moisture over a longer period of time than the climax communities. Vegetation on the fine textured soils withstood longer periods of drought than that in the sand dunes.

The tall grasses in the subirrigated meadows and the deciduous trees along the rivers have more available moisture than is afforded by rainfall because roots of these postclimax species receive moisture from the ground water.

Seasonal and daily fluctuations of the water table in the meadows result from trans-seasonal evaporation, and amount of water supplied by springs and seepage.

Drainage materially affects the amount of periodic fluctuation. Greatest fluctuations occur in the poorly drained lakes. Well drained lakes maintain a constant level in years of high rainfall; water from springs prevents marked lowering during drought.

River water has little salt in solution. Well drained lakes and swamps have fresh water; poorly drained lakes are saline.

Highest temperatures are on south slopes of dunes and in the prairie of hardlands. Environment on north slopes of the dunes and valleys is ameliorated by lower temperatures, less insolation, and protection from prevailing south winds.

Evaporation is highest on the tops of the dunes and lowest in the meadows and woodlands.

Submerged, floating and emersed aquatic plants are present in the fresh-water lakes and swamps. The chief plants are species of Potamogeton, Myriophyllum, Ceratophyllum, Typha, Sagittaria, Scirpus, and Phragmites.

Saline lakes have only a growth of algae. *Distichlis stricta* and *Scirpus americanus* grow on the shores and in the saline meadows.

Mesophytic tall-grass communities in the subirrigated meadows occur in three zones. A lower zone is flooded during the early part of the growing season. It is occupied by sedges (*Carex* spp.) and hydrophytic grasses, chiefly Calamagrostis. A middle zone is never flooded but water is near the surface throughout the year. Here tall grasses (*Spartina pectinata, Panicum virgatum, Sorghastrum nutans* and *Andropogon furcatus*) are dominant. The grasses in the upper edge of the meadow are too far above the water table to have access to ground water in autumn. They are dominated by true-prairie grasses and forbs.

Postclimax grasses grow on the dunes. *Redfieldia flexuosa* and *Muhlenbergia pungens* are pioneers in the blowouts. Muhlenbergia is a pioneer and persists in overgrazed dunes. *Andropogon hallii* is often a pioneer in blowouts and occurs only in small communities as fully developed vegetation. *Eragrostis trichodes* is able to dominate the north side of dunes in winter pastures, but, along with Andropogon, it is materially reduced as the result of selective grazing in most year-long pastures. *Calamovilfa longifolia* and *Sporobolus cryptandrus* are the most important range grasses. *Bouteloua hirsuta* and *Carex heliophila* are present, especially in the ground layer of mature communities.

Three stages in degeneration under grazing are evident. The most palatable grasses, such as *Andropogon hallii, Eragrostis trichodes,* and *Panicum virgatum,* are selectively grazed. *Calamovilfa longifolia* and *Sporobolus cryptandrus* become the dominant grasses in the second stage. In a third stage *Muhlenbergia pungens* and certain weedy forbs are common.

Ecological relations of the dominant grasses and forbs were understood only after the roots were studied. *Redfieldia flexuosa, Muhlenbergia pungens, Andropogon hallii,* and *Calamovilfa longifolia* have roots 4 to 8 feet deep and form an open growth by means of rhizomes 4 to 8 inches in length. All are tall grasses except *Muhlenbergia pungens.* It has essentially the same ecological position in its community with *Bouteloua hirsuta* as the tall grasses have in their respective communities.

The bunch grasses have shallow, but much branched roots. They spread widely in the surface soil but seldom penetrate more than 18 inches into the sand. *Eragrostis trichodes* forms tall bunches, *Sporobolus cryptandrus* is a mid grass, and *Bouteloua hirsuta* is a short grass. Short grasses form the major portion of the ground layer.

Forbs are of minor importance. Five major species are *Tradescantia occidentalis, Lygodesmia juncea, Artemisia gnaphalodes, Ambrosia coronopifolia,* and *Psoralea lanceolata.* These species are either drought enduring or drought escaping. Certain others are present only as pioneers in undeveloped communities where competition for moisture is not great. Some unpalatable species thrive in overgrazed pastures.

The bunches and stems of both grasses and forbs are widely and evenly spaced in the several communities. Basal area ranged from 1 to 3 percent.

The grass dominants flower in summer or fall, but growth takes place throughout the season according to occurrence of rain. Reactions to summer showers are more evident on the dunes than in the hardlands because of the differences in efficiency of absorption of water. The forbs bloom chiefly in spring and fall.

Five mixed-prairie grasses dominate fine sandy loam soils. The climax species are *Stipa comata* and *Carex filifolia. Bouteloua gracilis* increases greatly under grazing, *Buchloe dactyloides* is present only in overgrazed pastures. *Agropyron smithii* dominates the ravines where run-in water is received. It is a pioneer on abandoned fields.

Three stages in degeneration of mixed prairie are evident. *Stipa comata* is the first grass to disappear. In a second stage of degeneration *Carex filifolia* is destroyed and *Bouteloua gracilis* becomes dominant. In the final stage *B. gracilis* and *Buchloe dactyloides* are present with a large number of unpalatable forbs.

The chief forbs are *Aster ericoides, Artemisia caudata,* and *Listris punctata.* Other species such as *Artemisia frigida* and *Opuntia* spp. increase under heavy grazing.

Agropyron smithii and *Stipa comata* are mid

grasses; the others grow in short bunches. The mid grasses and *Carex filifolia* begin growth very early; the short grasses revive later. Greatest growth is made in spring. Flowering of the climax grasses takes place in May, and seeds are mature before mid-July. *Agropyron smithii* and *Bouteloua gracilis* flower in midsummer or later according to occurrence of rain.

Root layering in mixed prairie is not as evident as it is on the sand dunes. Roots penetrate 4 to 5 feet deep in the fine sandy loams. Basal cover was approximately 5 percent in climax vegetation (mixed prairie) but only 2 to 3 percent in disclimax communities of this association.

Ulmus americana, Fraxinus lanceolata, Acer negundo, and *Populus sargentii* are the major deciduous trees which grow along the banks of the river. Ponderosa pine occurs on the rough, stony lands in the valleys. Mixed prairie, true prairie, and certain Rocky Mountain shrubs and forbs alternate with the pine and often form an understory.

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SOME METEOROLOGICAL AND LIMNOLOGICAL CONDITIONS AS FACTORS IN THE ABUNDANCE OF CERTAIN FISHES IN LAKE ERIE

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SOME METEOROLOGICAL AND LIMNOLOGICAL CONDITIONS AS FACTORS IN THE ABUNDANCE OF CERTAIN FISHES IN LAKE ERIE

INTRODUCTION

During their development fishes are subjected to many variations in environmental factors. The integration of the individual effects of these changes produces fluctuations in population densities. Contributing to the degree of success of spawning, rate of survival of progeny, availability of food, and to the conditions encountered in migration, are the many ecological factors which together make up the complex environment. Among these factors are temperature, wind, precipitation, turbidity, light, currents, and substances dissolved in the water.

From month to month and from year to year meteorological and limnological conditions throughout Lake Erie vary. Fish populations change in density from year to year also, and persons familiar with the lake have associated these fluctuations with general weather and water conditions and speak of "good" and "bad" years as contributing more or less to fish numbers. Correlations have been sought between temperature and turbidity of the water, and precipitation, and numbers of some of the fishes. This is one of the many steps towards definition of the sets of conditions which result in highs and lows in populations of Lake Erie fishes.

Lake Erie is the most southerly of the Great Lakes, and is connected with Lake St. Clair by the Detroit River and with Lake Ontario by the Niagara River. It has a maximum length of 241 and breadth of 57 miles, and is at a mean elevation of 572.4 feet. The lake drains a basin of 34,680 square miles, and its own area is 9,940 square miles. It lies ENE by WSW for most of its length, but the head of the western end is more to the northwest. Point Pelee and Long Point, on the north shore, divide the lake naturally into three parts, of which the central is the largest. The western section is shallow, not exceeding 50 feet in depth, the central portion is intermediate with a maximum depth of about 80 feet, and the eastern division has an extreme depth of 210 feet; the average depth of the lake is 64 feet. Additional description of Lake Erie may be found in the literature (Fish 1929, Wright & Tidd 1933, Chandler 1940).

According to generally accepted theories of productivity, Lake Erie, partly because of its shallowness and southerly position in the chain of lakes, should be the most productive of the Great Lakes. This is substantiated by statistics on fish catches, which show that Lake Erie yields more fish than any of the other Great Lakes, about one third of the total (Van Oosten 1940). The commercial fisheries of Ohio are confined to Lake Erie, but in 1938 the poundage taken by Ohio fishermen was 27 percent of that taken by all other United States fishermen in the Great Lakes combined, and was exceeded only by the proportion caught by Michigan fishermen (35 percent). Most of the present investigation has been concerned with the pikeperches, Stizostedion. The percentages of yellow pickerel, *S. vitreum vitreum* (Mitchill), blue pike, *S. vitreum glaucum* Hubbs, and sauger, *S. canadense canadense* (Smith) taken in Lake Erie in 1938 amounted to 63, 99, and 90 respectively, of the total United States catch of each species in all the Great Lakes. The preceding evidence indicates the importance of the fisheries in Lake Erie in relation to the Great Lakes industry, and the predominance of certain species in the Lake Erie portion of the waterway.

To Dr. T. H. Langlois, Director of the Franz Theodore Stone Laboratory, are due my sincerest thanks. The active assistance of Dr. D. C. Chandler, and constructive criticisms offered by Dr. C. F. Walker, have aided greatly in shaping the course of the research and its presentation. Also, I am indebted to the Ohio Division of Conservation and Natural Resources for cooperation of personnel and use of records and equipment. I am pleased to acknowledge the personal interest and assistance given by several engineers, meteorologists, fishermen, and fisheries biologists.

METHODS

The Pearson product-moment coefficient, better known as the coefficient of correlation, has been adopted as a means of determining the effect of changes in average values of some physical factors upon fish catches in Lake Erie. Although greatest individual results may come from the action of temporary extremes, it is believed that that period of time in which occur the most unusually low temperatures, for example, will also have the lowest average temperature. Since critical phases in a fish's existence, for instance spawning, egg and fry stages, generally extend over a few weeks or months, and vary slightly in time of occurrence from year to year, the periods for which average factor values have been calculated are also of one or two months.

It is realized that correlation is only a special application of regression, and that the coefficient r is a measure of rectilinear relationship. There may be perfect correlation curvilinearly which would not be adequately measured by r; so, preliminary straight-line tests were sketched for nearly all correlations. Also, the concept of common elements has been kept in mind, but, following the lead of many workers, quantities expressed in different units have been correlated.

Tests of the significance of a coefficient have been according to the t test, based on the familiar null

hypothesis, or by comparison with a table of significance calculated according to the t test. Aids in calculation have been the slide rule, tables of logarithms, and an adding machine. (J. B. Clark 1932, Davenport & Ekas 1936, Simpson & Roe 1939, Snedecor 1940).

Sources of meteorological data have been annual station summaries issued by the Weather Bureau of the United States Department of Agriculture, and the northern Ohio section of a climatic summary (1936). Water temperature and turbidity data at Cleveland have been furnished through the kindness of Mr. Clyde H. Irwin of the Baldwin Filtration Plant; turbidities at several Lake Erie stations by Mr. T. R. Lathrop of the Ohio Department of Health; turbidity and plankton data at Put-In-Bay by Dr. D. C. Chandler; water temperatures at Erie, Pa., by Mr. J. S. Dunwoody, and at Buffalo, N. Y., by Mr. L. A. Bergman, superintendents of municipal water supplies.

Figures on fish catches in Lake Erie have been obtained from annual reports of the United States Bureau of Fisheries (Sette 1928, annual reports since then), and in Ohio from reports of the Division of Conservation (Wickliff 1939, Langlois & Edmister 1939, Edmister 1940, Langlois 1941).

RELATIONSHIPS BETWEEN FACTORS

Lake Erie extends in the extremes from 78° 51′ to 83° 29′ W. longitude and from 41° 20′ to 42° 54′ N. latitude. Within these confines it is quite possible that differences in air or water temperatures, or in other factors, may occur locally because of special occurrences such as the passage of storms. Of interest in the long-term trends, however, are average conditions over periods of one or more months. The investigation is concerned in part with whether or not different populations of fishes in different parts of the lake, or the same population moving from place to place, are subjected to average conditions which vary in the same direction, wherever the populations happen to be.

Air Temperature

Applying criteria of randomness of a series of observations to the mean annual temperatures at several Russian stations, Weinberg & Plamenevskij (1933) came to the conclusion that 75 km. is too big an average separation of the stations. Although the stations here employed, Toledo, Sandusky, Cleveland, Erie and Buffalo, are separated by an average of 110 km., the data are used for a slightly different purpose. It is not desired to see whether data from one station are so like the values obtained at its neighboring station that it would be permissible to omit the neighboring station from the records when regional averages are to be determined, but it is desired simply to show whether or not average monthly temperatures at five stations along Lake Erie fluctuate similarly with regard to direction from the mean of the averages of those months and not with regard to the actual amounts of the variations. It is believed that the results bear out the contention that the spacing of the selected stations from Toledo to Buffalo is satisfactory for the latter purpose.

From Toledo in the west, through Sandusky, Cleveland and Erie, to Buffalo in the east, average spring temperatures fluctuate similarly (Fig. 1). The westerly stations are also the most southerly, and the mean temperature decreases in order from the southwest to the northeast.

Water Temperature

At Cleveland and Erie, at the western and eastern extremities of the central portion of Lake Erie, fluctuations in temperature of the water in the months of April and May, 1927 to 1938, are related positively, with a statistically significant coefficient of correlation of 0.74. This relationship supports the hypothesis that average changes in water temperature are both general and in the same direction throughout most of Lake Erie. Average water temperatures for March, April and May at Cleveland and Erie are illustrated in Figure 2.

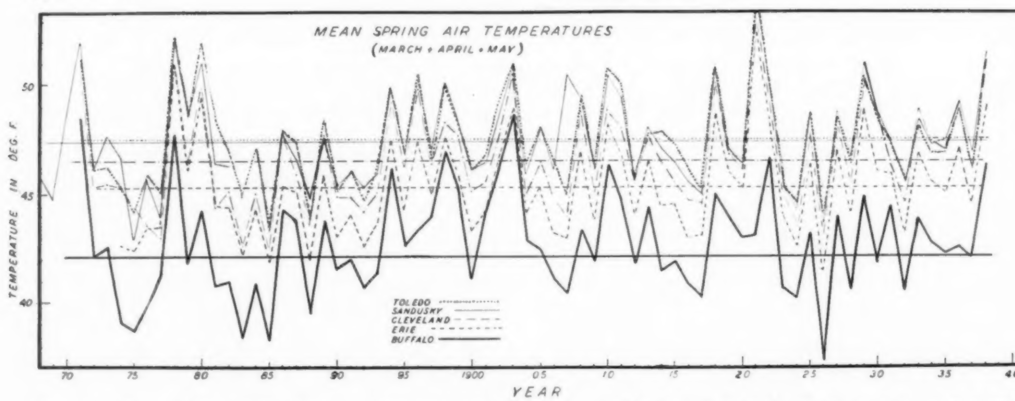

Fig. 1. Mean March-April-May air temperatures at Toledo, Sandusky, Cleveland, O., Erie, Pa., and Buffalo, N. Y., 1872-1938. The horizontal lines represent mean temperatures for the total period, and these temperatures decrease in order from west to east (Toledo to Buffalo).

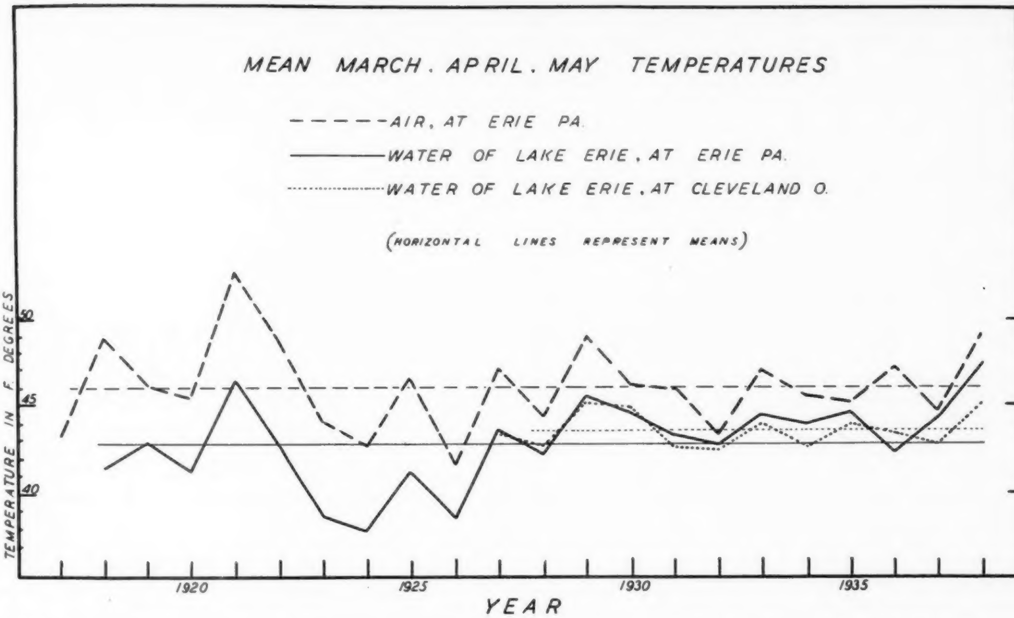

FIG. 2. Mean March-April-May temperatures of the air at Erie, Pa., of Lake Erie at Erie, and of Lake Erie at Cleveland, O. Temperatures of the water fluctuate as do those of the air, and water temperatures at different stations also vary similarly.

AIR AND WATER TEMPERATURES

The two media, air and water, both derive their heat primarily from the sun, so that factors affecting the amount of heat received from the sun will be reflected by the air and water together becoming warmer or cooler. Secondarily, air and water masses in proximity to one another exchange heat and so modify each other's temperature. Correlations have been drawn between the temperature of the sea from April to October and the temperature of the air in northern Europe during December to March of the following winter (Bergsten 1936). However, White (1934) has pointed out the error in accepting average air temperatures as representative of stream temperatures because of the influence of underground water.

Concurrent similar changes in air and water mean temperatures in the spring at Erie and in the summer at Buffalo are demonstrable. There is a statistically significant r of $+0.67$ between the average temperatures of the air and of Lake Erie in the months of April and May from 1918 to 1939, at Erie; the correlation coefficient is $+0.75$ for the same two variables in the months of June, July, and August between 1927 and 1938 at Buffalo (Fig. 2).

For the purpose of indicating variations from normal in monthly temperatures in corresponding periods from year to year either air or water temperatures may be used, since both fluctuate similarly. Where water temperatures were not available, those of the air have been employed.

PRECIPITATION

There is more local variation in precipitation than in temperature. Plamenevskij (1933), who used published data from third-order stations of the United States Weather Bureau in Ohio and Pennsylvania, came to the conclusion that a distance as great as 20 km., and perhaps up to 40 km., is admissible for the average distance between stations of such a network. A given number of meteorological stations would provide a much less complete specification of precipitation than of air temperature within a considered area (Hopkins 1938).

However, precipitations at stations (Toledo, Cleveland, and Erie) up to 150 km. apart along the south shore of Lake Erie also fluctuate together during the spring months. The March-April-May precipitations at Toledo and Erie are related with a statistically significant r of $+0.46$, from 1874 to 1938 (Fig. 3). In general, precipitation at several points along Lake Erie varies similarly during the spring months.

TURBIDITY

Lake Erie is characterized by extensive changes in turbidity, extensive both in degree and distribution. Turbidity values varied from 5 to 230 ppm. within one year in the Bass Islands region (Chandler 1942). During stormy weather the water of Lake Erie is uniformly turbid from surface to bottom in the shallow western end; after a few hours of calm the suspended materials, mostly inorganic matter, have

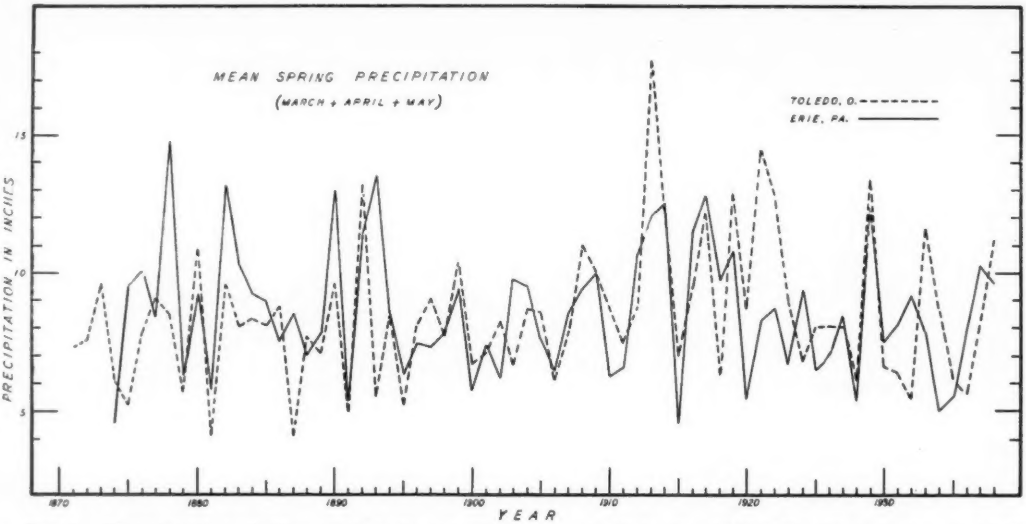

FIG. 3. Mean March-April-May precipitations at Toledo, O., and Erie, Pa., 1874-1938. There is a r of +0.46 between these variables.

settled in part, so that the upper waters have become less turbid than the lower.

Horizontal variations in turbidity of Lake Erie are less well known. From the air, streaks of relatively clear and turbid water may be seen in juxtaposition; also, travel by boat north and east from the Bass Islands generally shows less turbid water than in the immediate island region. There are fluctuations from year to year in average April-May values of the turbidity of Lake Erie at Port Clinton, Huron, Cleveland, and Ashtabula, but most of these variations go up and down together at all the stations (Fig. 4). Therefore, in spite of local vertical and horizontal differences, all of Lake Erie becomes more

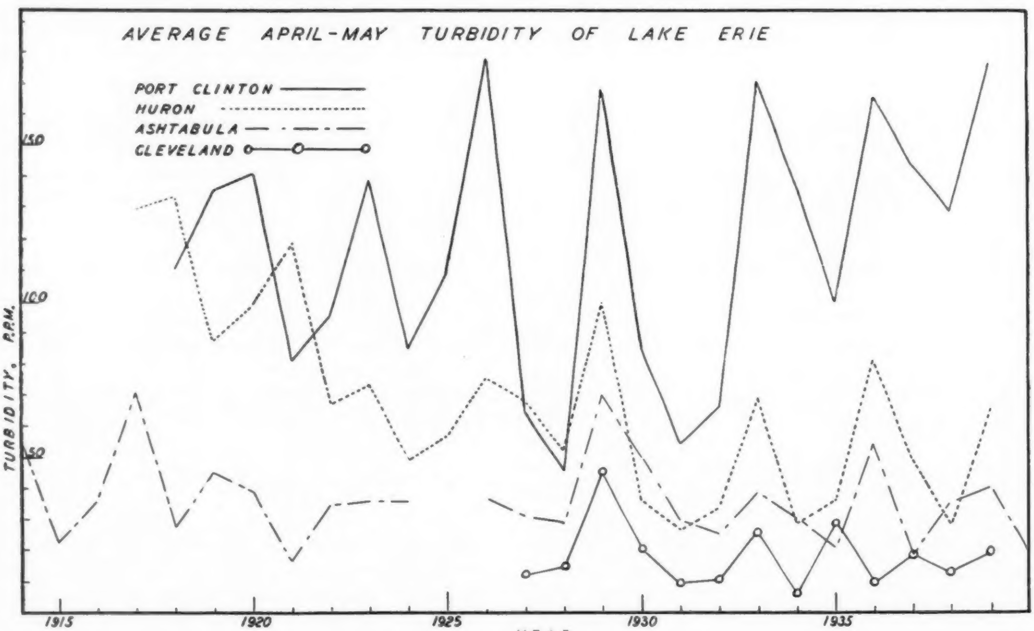

FIG. 4. Mean April-May turbidities of Lake Erie at Port Clinton, Huron, Ashtabula and Cleveland, O. The turbidity is greater in the western part of the lake. The Cleveland values are low because the samples are taken from several miles offshore.

or less uniformly muddier or clearer over certain months. The western part of the lake is more turbid than the eastern, and water off Cleveland appears less turbid than at Ashtabula only because the Cleveland samples are drawn from several miles offshore.

PRECIPITATION AND TURBIDITY

The observation that streams not only rise but become more turbid after rainfall is familiar. The effect of precipitation upon lake water is not quite so noticeable. The rivers tributary to western Lake Erie, draining cultivated farmlands, bring suspended as well as dissolved matter into the lake. Variations in precipitation are responsible for most variations in the amount of run-off (Prior 1929), and hence should bear some relation to turbidities in the lake, especially in the shore waters.

In the absence of stream flow records, and, rather than a measure of precipitation only at the mouth of a river, a more accurate conception of the amount of precipitation in the river's drainage basin may be obtained from records at several scattered stations in the area. Analysis of the data (Weather Bureau 1936) reveals that in the Maumee River basin there is an r of $+0.58$ between the March, April, and May precipitation at Napoleon, Defiance, Ottawa, and Findlay over a period of 14 years, and that at Toledo (1906-11, and 1923-30; records not available for Defiance, 1912-22). Also, there is a highly significant r of $+0.74$ between similar precipitations at Fremont, Tiffin, and Upper Sandusky in the Sandusky River drainage and that at Sandusky at the river's mouth, from 1906 to 1930. This suggests that there is probably no serious drawback to the employment of average precipitation data for a station at a river mouth only, in further correlations between precipitation and lake turbidity.

Currents play an important part in distributing suspended matter in the lake. Harrington (1895) has shown that there is a surface drift from west to east, and that current is rather better marked along the south than the north shore of Lake Erie. Unpublished data on file at this laboratory indicate that winds are the dominant determinants of the direction of flow. Flowage along the south shore in western Lake Erie should be eastwards in the spring, since the winds have a prevailing westerly component. In addition, the trend of the water mass of the lake must be towards the outlet, i.e. from west to east.

It is now justifiable to compare water turbidities at Cleveland with precipitation there and to the westward, since it is quite probable that most of the water at Cleveland comes from the west where a number of turbid rivers flow into the lake. The mean April-May turbidities of Lake Erie at Cleveland have borne a significant relationship ($r = +0.60$) to the average precipitations in those months at Toledo, Sandusky, and Cleveland, from 1927 to 1938. There is the possibility that the mechanics of the relationship may involve not only increased debouchments of suspended matter by the westerly rivers when the precipitation is high, but may involve more obscure interactions between precipitation, storms, heavy wave action, and turbidity.

TURBIDITY AND PLANKTON

Suggestive evidence of how changes in turbidity of the water may affect fish production by affecting plankton distribution has been provided in data made available through the kindness of Dr. D. C. Chandler (Table 1).

TABLE 1. Turbidities, and mean percentages of zooplankters in surface portion of collections from depths of 0, 5, and 9 meters in western Lake Erie. Twenty-six samples were taken between Sept. 2 and Dec. 15, 1938, and Aug. 31 and Nov. 4, 1939. Data by Dr. D. C. Chandler.

Turbidity ppm.	Number of days	Mean percentage frequency of organisms in 0 portion of total 0+5+9 meter samples				
		Daphnia	Bosmina	Diaptomus	Cyclops	Nauplii
15 – 30....	15	2	23	11	18	37
35 – 60....	11	7	26	19	25	36

From September to December, 1938, and during September and October, 1939, quantitative plankton samples were taken at 26 regular intervals at one station in western Lake Erie. These periods include two autumn pulses. Of the 26, on 15 there were water turbidities of 15 to 30 ppm., and on 11 days there were turbidities of 35 to 60 ppm. Most of the zooplankters were more concentrated in the upper one meter of water on turbid than on clear days. Fish that ate plankton would perhaps find better feeding conditions near the surface when the water was highly turbid.

TAGGING AND MIGRATIONS

Tagging and recovery of individually marked fishes provide two points at which a fish was present during its movements about a lake—the place of release, and, separated by a known interval of time, the place of recovery. If lengths were recorded each time a fish was handled, additional information on growth rate is available. Large numbers of recoveries enable an investigator to determine the distance and direction of movement of the majority of a population. In this manner, shifts from one locality to another, mostly seasonal, become definitely known from individual records. Tagging at widely separated localities also will indicate whether or not there are separate populations of fishes in the same body of water; it will assist in demonstrating if fishes which appear morphologically similar behave the same physiologically. In addition, in conjunction with a measure of the total catch, estimate may be made from the proportion of tagged fish in the catch as to the approximate standing crop in the lake.

Three kinds of tags have been evolved. The earliest, and still used for some marine fishes, consists of two buttons of vulcanite or hard rubber connected

by silver wire. Passing through the fish, the wire holds a button against each side of the body. The strap or clip tag is a light metal clip which is bent in a U shape and locked in place with special pliers; it is generally attached to a gill cover, caudal peduncle, or fin. Of more recent development is the metal or celluloid flat oval piece which is placed internally through a slit in the abdomen, and recoveries are made during processing or cleaning a fish. Common to all tags is a serial number and some indication of a forwarding address. Strap tags, attached to a gill cover, were used in the present work.

Returns from fish tagging operations have varied widely, according to the type of tag used, the care given to its application, the effort expended on getting data on recaptures, and to the survival of the fish tagged. Eastern Atlantic salmon have been retaken, after tagging, to the amount of 0.4 percent off Esthonia (Reinwaldt 1938), and in amounts of 13, 23, and 12.5 percent off the Scottish coast (Menzies 1938, 1938a). In the Pacific, returns have been recorded of 5.2 percent for mackerel (D. H. Fry 1937), and about 25 percent for the sardine off California (Janssen 1938); and of 5.3 to 15.5 percent for spring salmon (Clemens *et al.* 1939), and of 7.3 percent for herring (Hart & Tester 1939) and of 1.0 to 17.4 percent for pilchards (Hart 1939) off British Columbia. Vladykov & Wallace (1938) found that 42.4 percent of striped bass tagged in Chesapeake Bay were caught within nine months of release. In fresh waters, Shetter (1937) reported that 24.3 percent of tagged brook, brown, and rainbow trout in a Michigan river were retaken, Doan (1937) that 25 percent of a planting of tagged adult lake trout, and Eschmeyer (1942) that an average of 19.6 percent of tagged individuals of several species in Norris Reservoir were reported recovered. General tagging in Michigan, using strap tags, yielded a return of 2.71 percent (Shetter 1936).

TABLE 2. Fishes tagged in Lake Erie, according to species, locality, and year of release.

Species	Year of tagging 1938	1939	1940	Totals	Number of returns	Per cent returns
A. fulvescens Rafinesque	5	1	2	8	0	...
C. carpio Linnaeus	39	27	1	67	2	3.0
I. l. lacustris (Walbaum)	113	68	39	220	2	0.9
P. flavescens (Mitchill)	38	493	77	608	13	2.1
S. v. vitreum (Mitchill)	369	414	465	1248	22	1.8
S. v. glaucum Hubbs	649	272	17	938	20	2.1
S. c. canadense (Smith)	1	43	22	66	6	9.1
M. d. dolomieu Lacepede	14	40	63	117	9	0.8
A. grunniens Rafinesque	44	83	10	137	1	0.7
Others	30	296	26	352	9	2.6
Totals	1302	1737	722	3761	84	2.2
Locality of release						
Bass Islands, O.	661	825	249	1735		
Conneaut, O.	428	261	....	689		
Port Crewe, Ont.	213	....	....	213		
Sandusky Bay, O.	....	287	....	287		
20 mi. NE Cedar Point, O.	....	364	....	364		
10-12 mi. NW Port Clinton, O.	....	....	429	429		
West Sister Is., O.	....	....	44	44		
Totals	1302	1737	722	3761		

In Lake Erie, 3,761 fishes were tagged during 1938, 1939, and 1940. Individuals of 22 species have been marked, but most attention has been directed toward eight species amounting to 90 percent of the total tagged. Yellow pickerel and blue pike together constituted 58 percent of all the fish tagged (Table 2). Fish tagged near the islands in western Ohio waters, those along or opposite the central part of the Ohio shore, and those of eastern Ohio have amounted to 59, 23, and 18 percent, respectively, of the total marked (Table 2).

Returns to January 1, 1942, have totalled 84, or 2.2 percent of the number tagged (Table 2). Of these recoveries, half were made within one month, two thirds within six months, and 95 percent within one year of release (Table 3).

Most marked fishes did not travel very far in the first two weeks after release (Table 3), and small-

TABLE 3. Recoveries of tagged fishes in Lake Erie. Distances travelled, according to time elapsed between release and recovery. The figures in parentheses represent the number of recoveries.

Species	DISTANCE IN MILES 0 – 1 week	1 – 2 weeks	2 – 4 weeks	1 – 2 months	2 – 6 months	6 – 12 months	1 – 1½ years	1½ – 2 years	2 – 3 years	Total recoveries
Megastomatobus cyprinella (Val.)	....	....	....	....	....	0 (1)	..	....	..	1
Catostomus c. commersonnii (Lac.)	0 (1)	....	....	....	17 (2)	30 (1)	..	....	..	4
Cyprinus carpio L.	....	....	0 (1)	....	....	34 (1)	..	....	..	2
Ictalurus l. lacustris (Wal.)	....	....	....	....	....	....	..	15 (2)	..	2
Perca flavescens (Mitch.)	0.6 (5)	2 (2)	....	15 (3)	....	9 (3)	..	....	..	13
Stizostedion v. vitreum (Mitch.)	1 (5)	....	20 (3)	16 (1)	32 (5)	25 (9)	..	200 (1)	..	22
Stizostedion v. glaucum Hubbs	0 (3)	0 (6)	22 (2)	....	46 (3)	31 (5)	..	80 (1)	..	20
Stizostedion c. canadense (Smith)	....	4 (1)	8 (4)	....	....	17 (1)	..	....	..	6
Micropterus d. dolomieu Lac.	9 (3)	....	12 (5)	....	2 (1)	....	..	....	..	9
Ambloplites r. rupestris (Raf.)	0 (1)	....	....	....	....	0 (2)	..	....	..	3
Lepibema chrysops (Raf.)	....	....	....	0 (1)	....	....	..	....	..	1
Aplodinotus grunniens Raf.	....	....	....	....	....	4 (1)	..	....	..	1
Average	2 (18)	1 (9)	13 (15)	12 (5)	30 (9)	20 (24)	..	78 (4)	..	84

Per cent of total recoveries ... 50 — 17 — 29 — 5

67 — 33

95

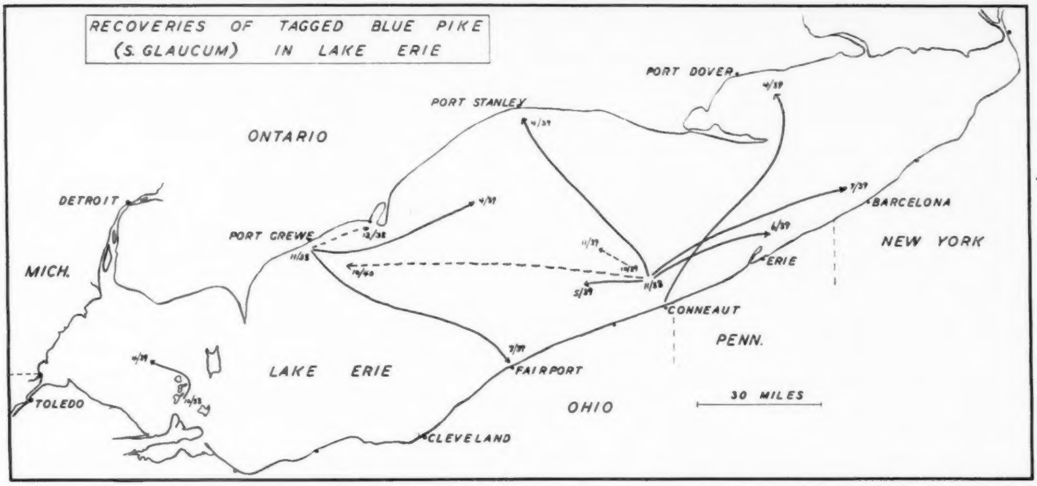

FIG. 5. Map of Lake Erie showing locality, month and year of releases and recoveries of tagged blue pike *(S. vitreum glaucum)*.

mouth bass, *Micropterus dolomieu dolomieu* Lacepede, were the most active. Average distances of movement increased up to six months, and decreased between six months and one year. The latter is to be expected, because after six months yellow pickerel and blue pike, for which species the records are most numerous, should again be on their way back to localities which they visited at the time of tagging.

Most of the returns on blue pike were from those tagged in the latter part of the year near Conneaut, O. (Fig. 5). There were few fishes recaptured at any great distance from Conneaut in the autumn; however, the trend was westward. During the spring that followed release, tagged fish were reported along both shores of the central and eastern parts of the lake, and along the edge of the deeper portion of Lake Erie in summer, between Erie and Barcelona. Fishes tagged in the autumn at Port Crewe, Ont., were taken eastward the next spring and summer. In general, blue pike move westward from central Lake Erie in the autumn and winter, shoreward in the spring, and to the region of deep water in the summer. From the west-central part of the lake, movement is eastward in the spring and summer.

The yellow pickerel is a fish of western Lake Erie, but the greatest minimum distance travelled by a member of this species yet recovered was traversed when a yellow pickerel went from South Bass Island, O., to Irving, N. Y., about 200 miles (Fig. 6). Pickerel tagged near the islands in the autumn were

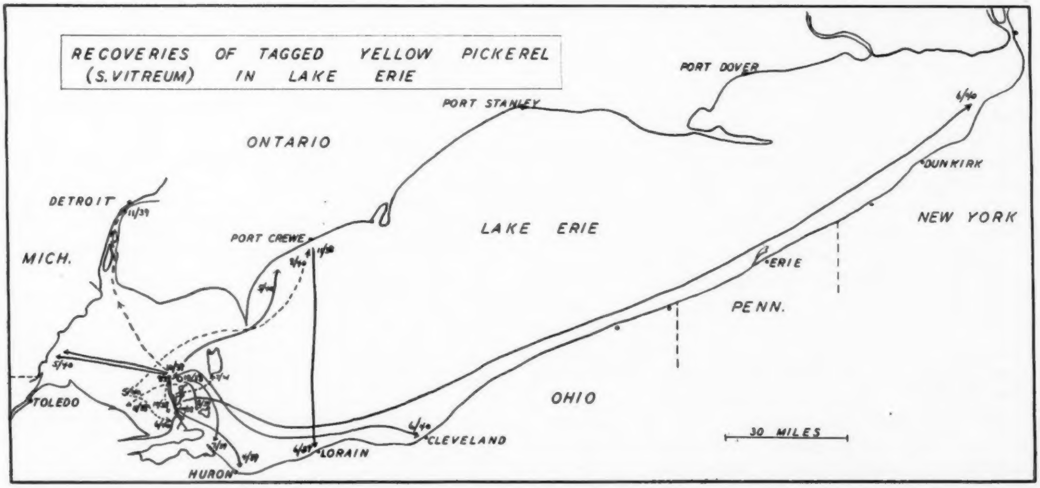

FIG. 6. Map of Lake Erie showing locality, month and year of releases and recoveries of tagged yellow pickerel *(S. v. vitreum)*.

retaken westward along the mainland shore and one up the Detroit River, in the same autumn. In the spring, fishes from autumn taggings were reported along both shores and the end of the western portion of the lake. In the summer, fishes marked near the islands in both the autumn and spring were caught eastward toward and in the central part of the lake.

Recaptures of other species have been too few to draw any but tentative generalizations from the data. Channel catfish, *Ictalurus lacustris lacustris* (Walbaum), keep to the western part of the lake; rock bass, *Ambloplites rupestris rupestris* (Rafinesque), show little or no movement; sauger go north and west from the islands in the autumn; some smallmouth bass go west the same autumn, and north and west the same spring of tagging in the island region; the common white sucker, *Catostomus commersonnii commersonnii* (Lacepede), travels southeast in the spring and west in the summer from the islands; and yellow perch, *Perca flavescens* (Mitchill), are taken westward of the islands in the spring after the autumn of tagging.

Chidester (1924) has attributed to temperature the greatest importance as a cause of fish migration, because it affects the chemical processes of the environment and has a profound influence on the rate of metabolism of fishes and on their responses to external stimuli. A fish's awareness of changes in temperature is through corpuscles in the skin which react to heat and cold. Wells (1914) found all species of fishes equally sensitive to variations in temperature of one C.°, while Bull (1937), using conditioned response technique, found that changes of as little as 0.03 to 0.10 C.° brought about a reaction. In his monograph, Chidester (1924) also outlined the role of other factors in fish movements, and observed that developing gonads may create a demand for a new environment with different amounts of O_2, CO_2, or lactic acid. Other contributing agents to migration may be the search for food, pollution, currents, and a moving optical field. The lateral line is not of great importance. Olfactory, gustatory, chemical, tactile, and kinesthetic senses may be brought into use.

Migrations of Atlantic salmon into fresh waters have been attributed to good feeding, fatness, and an abrupt fresh to salt water gradation (Huntsman 1933). Powers (1941) has recently developed a theory to explain salmon movements, in which the physico-chemical behavior of mixed fresh and sea waters produces a carbon dioxide gradient which is the dominant factor in determining fish action. Changes in sea and river temperature, river flow, and surface currents in the sea are correlated with the salmon spawning migration in the White Sea (Danilcenko 1936). Changes in temperature are also of great importance in bringing about movements in ciscoes (F. E. J. Fry 1937), lake trout (Fry & Kennedy 1937), cod (Schroeder 1930), and in the seaward migration of young sockeye salmon (Foerster 1937).

COMMERCIAL CATCH AS A MEASURE OF ABUNDANCE

There is no practical method of determining directly the number of fishes in Lake Erie. Only estimates can be made, and these are best based on the number of pounds of fish taken per unit of fisherman effort. The unit of effort is one lift of a trap net, or one lift of 1,000 yards of gill net. This measure of abundance is really one of availability, and assumption is made that when fishes are easily caught it is because they are abundant.

If the amount of gear does not change greatly, then it may be expected that peaks and depressions in total catches from year to year indicate actual fluctuations in abundance. The yearly average of the number of pounds of striped bass taken daily by each boat in the California fishery (G. H. Clark 1933) so closely follows annual total production that the latter may be accepted as a fairly good index of abundance.

For the yellow pickerel fisheries of parts of Lake Huron and Lake Michigan, Hile (1937) has calculated indices of abundance based upon average catches per unit of effort for each type of gear engaged in the fisheries. A representation of Hile's findings illustrates that fluctuations in production, abundance, and the annual catch made by the principal type of gear approximate each other from year to year (Fig. 7).

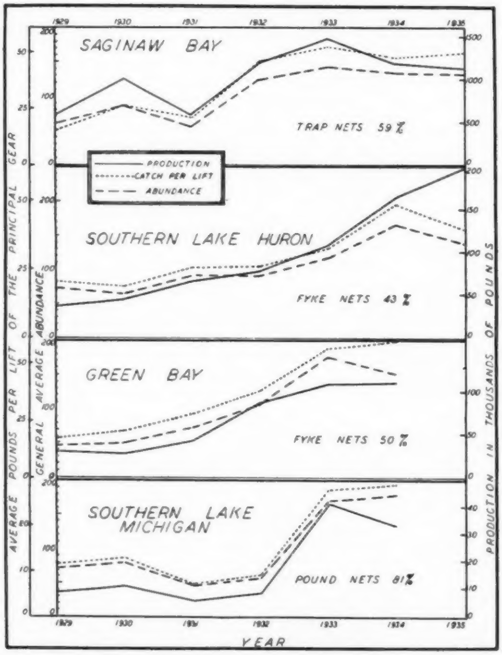

FIG. 7. Illustration of the relationship between production, abundance and the annual catch made by the principal type of gear engaged in yellow pickerel *(S. v. vitreum)* fisheries in Lake Huron and Lake Michigan (data from Hile, 1937).

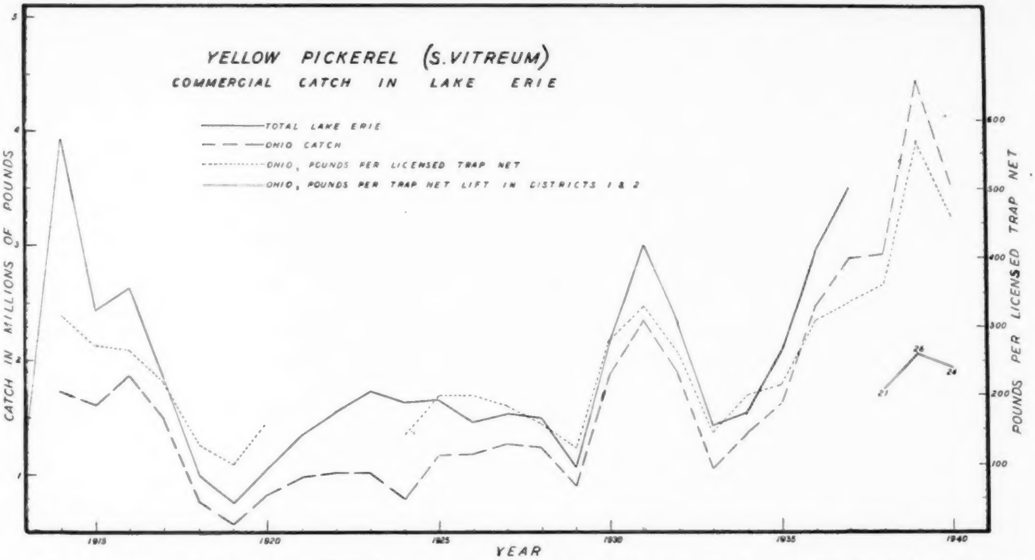

FIG. 8. Fluctuations in the commercial catch of yellow pickerel *(S. v. vitreum)*. Changes in the total pickerel catch of Lake Erie, that of Ohio, and the number of pounds of pickerel per licensed trap net have been in harmony.

The Lake Erie fisheries are similar to those of Lake Huron, and trap nets catch over 93 percent of Ohio's annual production of yellow pickerel (average 1935-40). Since 1914, fluctuations in the total yellow pickerel catch of Lake Erie, that of Ohio, and the number of pounds of pickerel per licensed trap net have been in harmony (Fig. 8). The average number of pounds of pickerel taken per trap net lift in the central and western Ohio fishing grounds was 21 in 1938, 26 in 1939, and 24 in 1940. These last measures, supposedly the most nearly ideal method to determine relative abundance in a commercial species (Hile & Duden 1934), are in accord with the fluctuations in total catch. Throughout this paper, presumption has been made that total catch is as good an index of abundance of other Lake Erie species as it is of yellow pickerel.

RELATIONSHIPS BETWEEN FACTORS AND FISHES

It is realized that no factor alone determines the success or failure of survival and growth of a fish population, but that many factors have an influence. If a fish is well adapted to its environment, the ranges of values of the factors should be near the optimum for, or within the range of tolerance of, the fish. If a fish is not perfectly adapted to its medium, and few are, it may be poorly adapted by virtue of being a recent immigrant into new ranges, or by virtue of changes in the environment so rapid that biological readjustment has not yet approached perfection.

Adjustment of a fish to its environment may be quite satisfactory with the exception of one or two inimical factors. A given factor may be so important a control that its variations are reflected in similar variations, in like or opposite phase, in the size of a fish population. It is proposed to investigate a few of the possible factors separately in regard to their effect on some fish populations in Lake Erie.

TEMPERATURE

The killing of fish by unusually low water temperatures has been demonstrated (Johansen 1927, Lumby & Atkinson 1929, Dannevig 1930, Storey 1937, Gunter 1941). Further complications of a seasonal nature may be involved in the cold effect; sturgeon placed in a state of anabiosis, produced by low temperature, revived in the autumn, but they did not revive when cooled in the summer (Schmidt & Platonov 1938). Deaths of fishes because of excessive heat *per se* have not generally been so attributed, since chemical derangements of both the water and the fishes generally accompany the high temperatures and offer explanations of the causes of death.

Reductions in numbers of fish food organisms by excessive heat or cold may play a part contributory to the ultimate decrease of predatory fishes. Leonard (1939) showed that unseasonal freezing of a small pond in southern Michigan probably significantly reduced the population of *Chironomus plumosus* which were imbedded in the ice while preparing to transform. The formation of anchor ice may have similar deleterious effects.

Temperature is more important to aquatic than it is to terrestrial animals, since the average range over which development is possible in the former is 14° C. and is 24° C. in the latter (Moore 1940). Fishes

require a very narrow range of temperatures, which varies with the species, in which to accomplish reproduction successfully (Tibby 1937). With increased temperature there is a direct decrease in the time of hatching (Johansen & Krogh 1914), but this increased hatching rate varies for different species (Embody 1934). Bonnet (1939) has pointed out that a cod egg at some stages is more susceptible to death than at others; but Nakai (1927) had drawn the conclusions that within the limits of favorable temperatures the eggs of *Leuciscus hakuensis* are often very little damaged before they hatch, but in unfavorable temperatures many dead eggs are observed at early embryonic stages.

The effect of variations in temperature during incubation also has some importance, since variations, too, occur in natural water temperatures. Using *Ambystoma punctatum* embryos, Buchanan (1939) reported that regular variations over short intervals produced the same results as did the constant mean temperature, but that variations from high to low temperatures at 24-hour intervals promoted faster growth and development in the embryos than did a steady mean temperature. Increases in the mean variation of temperature produced an increase in the hatch rate of rainbow trout, and similar mean increases resulted in faster death rates and decreases in the survival days of sockeye and dog salmon fry (Kawajiri 1933). Therefore, it might be expected that wide daily variations in Lake Erie's water temperature would result not only in faster hatching of eggs, but also in a greater death rate of the embryos and fry.

Water temperature has considerable influence over the success of fishing, because it affects the catch at the time of adverse or favorable temperatures, and it promotes a large or small crop of young fishes some years previous to the fishing operations. The importance of a restricted optimum range of water temperature has been shown for good cod fishing (Sleggs 1932, McKenzie 1934, H. Thompson 1935), for haddock (Vladykov 1933), and for herring fishing (E. Ford 1930). The presence of dominant year classes in stocks of fishes (Scofield 1931, F. N. Clark 1939, P. M. Hansen 1939, Doan 1940) has been associated with inquiry as to what unusually favorable conditions prevailed at the time of the hatching of the class which later became dominant. Temperature has been used or suggested as an aid to forecasts of the magnitude of catches of anchovies in Holland (Fowler 1890), Alaskan herring (Rounsefell 1930), mackerel and silver-eel in the southern Baltic (Jensen 1939), and herring in the North Sea (Carruthers & Hodgson 1937).

Whitefish.—A large part of a year's total catch of whitefish (*Coregonus clupeaformis latus* Koeltz) in the Ohio waters of Lake Erie is made in November and December; the catch in these months amounted to 49 and 69 percent of the total for the species in 1940 and 1939. No significant correlations have been found between the mean autumn (Nov.-Dec.) air temperatures as measured at Sandusky and the weight of the Ohio whitefish catch in the same year, throughout the period 1921-38 and the period 1915-38. Of fish-cultural interest, there is a rather close relationship between low water and air temperatures and high fertility and increased receipts of whitefish eggs at the Put-In-Bay hatchery (Wickliff 1933).

Yellow perch.—The eggs of yellow perch are spawned and hatch in April and May. Mean April-May air temperatures at Toledo, Sandusky and Cleveland bear no significant correlations with Ohio commercial catches of the species one, two or three years later, from 1914 to 1939.

Yellow pickerel.—Temperatures in spring have shown no relation to sizes of catches of yellow pickerel. Mean April-May air temperatures at Cleveland, Sandusky and Toledo have non-significant r values with Ohio catches of yellow pickerel in the same year, and with catches made three or four years later, from 1914 to 1938.

Blue pike.—The Ohio catch of blue pike in Lake Erie is made mostly off the central and eastern shores of the state. Nearly four fifths of the annual catch of this species was taken in these waters in 1939 and 1940. Over half the total pike was caught in May and June, and these months also include the time of spawning and early fry stages of these fishes in the eastern part of the lake. The results of a factor which operates upon the survival of fry should be evident after such time as the young fish have grown up and have entered the commercial fisheries. Two-year-old blue pike constitute the bulk of the catch (Table 4).

TABLE 4. Numbers of individuals, according to year groups, in samples of yellow pickerel, blue pike, sauger, and yellow perch taken commercially in Lake Erie.

Year of sample	Annuli 1	2	3	4	5	6	7	8	11
					YELLOW PICKEREL				
1937	.....	.....	6	51	31	7	.....	3	.....
1938	.....	62	120	119	46	15	3	.....	1
1939	.....	.....	251	153	39	14	10	.....	.....
1940	.....	26	30	4	2	.....	.....	.....	.....
					BLUE PIKE				
1937	.....	.....	5	4	2	1	.....	.....	.....
1938	2	345	77	32	8	.....	1	.....	.....
1939	.....	.....	167	8	1	.....	.....	.....	.....
1940	.....	263	237	8	.....	.....	.....	.....	.....
					SAUGER				
1937	.....	.....	12	10	.....	.....	.....	.....	.....
1938	.....	1	10	26	5	.....	.....	.....	.....
1939	.....	.....	140	32	2	.....	.....	.....	.....
1940	2	52	40	3	.....	.....	.....	.....	.....
					YELLOW PERCH				
1937 to 1940	4	333	253	428	35	1	.....	.....	.....

Temperature variations affect the stock of blue pike, because they change the vulnerability of adults to capture, and influence spawning and fry survival. In the former, evidence of the temperature effect should be seen in the year of the catch. However,

there is almost no correlation between the mean May-June air temperature at Cleveland and Erie and the size of the Ohio catch of blue pike in the same year, over the period 1914-38.

On the other hand there is a relation between May-June temperature and blue pike catch two years after the year of the temperature (Fig. 9). If Y represents the Ohio commercial catch of blue pike in tens of thousands of pounds, and X the mean May-June air temperature at Cleveland and Erie two years previous to the catch, then $Y = 64.6 X - 3404$. Or, using correlation methods, there is a statistically significant r of $+0.49$ between these variables. Using the regression equation, an attempt was made to estimate, before the commercial fishing reports for 1940 had been compiled, what the total blue pike catch for that year would be. The estimate was about 15 percent higher than the actual catch.

Sauger.—Search for relationships between temperatures and Ohio sauger catches have not yielded significant correlations. Positive non-significant r values were obtained between April-May air temperatures at Cleveland, Sandusky and Toledo and catches of sauger three years later for the years 1914-39, 1914-23, and 1924-39; between mean March air temperatures at the same stations and catches three years later for 1914-23 and 1924-39. Sauger of three years of age constitute the dominant year class in the fishery in most seasons (Table 4). Apparently higher temperatures in the spring somewhat favor increased production three years later, but only to a limited extent.

Total catch.—If there is any relation between temperature and the size of the total Ohio catch some years later, then the findings may point toward a principle of general biological importance involving increase and decrease in total activity in the lake. Greater or lesser poundages in the commercial catches would only be one evidence of general activity, this one phase involving changes in rate of growth and weight accumulation.

Average April-May water temperatures at Erie, from 1918 to 1938, have been correlated with total Ohio catches one, three and five years later, with coefficients of $+0.42$, $+0.31$ and $+0.28$ respectively. Of the three, the relation between catch and temperature the previous year is almost at the 5 percent level of significance (0.43 would be significant).

TURBIDITY

Many researches involving inter-relationships between survival and growth of fishes and turbidity of the water have concluded that any degree of turbidity, especially the higher values, is generally inimical to the fishes. It is the exceptional report that admits that turbidity may have a beneficial effect. In shallow ponds and bays higher aquatic plants in moderate amounts may indirectly add to the density of fish populations. High turbidities in such places would decrease the transparency of the water and prevent the plants from receiving sufficient sunlight (Meyer & Heritage 1941, Jones 1938). In deeper lakes submerged plants are of less importance; here, phytoplankton, capable of moving towards or away from the surface of the water, can exist in spite of high turbidity.

The action of schools of carp in "working up" the water is a familiar observation. Other fishes have been thought to do likewise; the complete poisoning of a fish population, 79 percent of which were black bullheads and redmouth buffalo, resulted in the clearing of water formerly turbid (Thompson & Bennett 1939). Similarly, crayfish control vegetation in ponds because they keep the waters turbid (Langlois 1936).

Less consideration, however, has been given to the agency of aquatic animals as producers of turbid water than to the effects of turbidity upon the animals. It was shown that increased turbidity in Lake Erie results in a greater proportion of zooplankters near the surface than at times of less turbidities. The essence of work on the Rogue River drainage is that muddy water is not seriously detrimental to aquatic life, including fishes (Ward 1938); in addition to protecting fishes from the sight of predators, mostly anglers, the suspended particles may serve as substrate for the formation of bacterial colonies which, when ingested, would provide nourishment for fishes and invertebrate organisms.

Yellow perch.—No significant relation has been demonstrated between average turbidity values of Lake Erie water at Cleveland in April and May, 1927-39, and the Ohio commercial catch of yellow perch in the same year, and one, two, three or four years later. Two-, three-, and four-year-old perch constitute the bulk of the commercial catch (Table 4), and most spawning takes place in April and May. Lack of positive evidence does not delete the possibility that turbidity may affect perch abundance, but, as yet, no direct connections between the two have been established.

In spawning, the eggs of yellow perch are given out by the female while she swims freely through the water. The eggs are in a gelatinous string, much like those of the common toad, and are not broadcast individually as are those of the yellow pickerel. Perch favor regions of underwater vegetation as spawning grounds, and the strings of eggs are draped about the plants, to which they adhere. Langlois (1941a) has emphasized the principle that Lake Erie is a changing habitat, and has made reference to data which indicate that one of the factors is a gradual decrease in formerly extensive beds of aquatic vegetation, accompanied by increases in turbidity. This disappearance of vegetation has substituted second-rate spawning grounds for perch, and the indirect connection with turbidity is evident.

Yellow pickerel.—Fishermen remark that in the spring months they make better catches of yellow pickerel when the water is clear than when it is muddy. This observation is confirmed by the finding of a significant r of -0.64 between the April-May mean turbidities of Lake Erie at Cleveland, 1927-36, and the Ohio commercial catches of pickerel in the same years. Low turbidities act upon pickerel with

little biological importance, except that they serve as accessories in the reduction of the stock.

Blue pike.—High turbidity mean values of Lake Erie water, as measured at Cleveland in April and May, also reduce the Ohio commercial catch of blue pike both in the same year and two years later, from 1927 to 1937. However, the correlations are not significant.

Sauger.—The greater part of the sauger catch in Ohio is taken in the spring, and saugers have the greatest availability as early as nets can be operated in April (Langlois 1941). Three-year-old sauger are usually dominant in the commercial catch. If turbidity is a factor in the sauger's abundance, then the magnitude of the catch should bear some relationship to turbidities three years previous in the months of April and May when spawning and hatching occur. This relationship may be expressed in the statistically significant r of $+0.79$ between average April-May mean turbidities of Lake Erie at Cleveland, from 1927 to 1936, and the Ohio sauger catch three years later. This correlation between turbidity and sauger catches has been dealt with more fully elsewhere (Doan 1941), and it was suggested that higher turbidities may act to prevent stickiness in sauger eggs, may give young fry protection from predators, and may facilitate the young saugers' feeding by concentrating plankton organisms near the surface.

Total Ohio catch.—High spring turbidities are associated with decreases in the total Ohio catch in Lake Erie, a statistically significant coefficient of correlation of -0.70 being in operation between the mean April-May turbidity of the lake at Cleveland and the total commercial catch of all species in the same year, from 1927 to 1939. From this, it would seem that muddy water in the spring months does not favor all fishes, and added significance is given to the special effect of turbidity upon later sauger catches.

PRECIPITATION

The effects of precipitation are more apparent upon land plants and animals than upon aquatic organisms. In the more arid districts of southwestern United States trees are much dependent upon rainfall in order to make good growth, and positive relationships have been established between rainfall and tree ring width (Douglass 1931). Even in more humid regions, growth of Tsuga and Juniperus is dependent upon precipitation (Lyon 1936, Hawley 1937). At high elevations the effect of precipitation upon growth of trees is less marked, and temperature fluctuations are more important (H. P. Hansen 1938).

Agricultural research is concerned, in part, with studies of crop-weather observations in efforts to forecast yields of the more important crops (Sarle 1940). Corn yields from Texas to Nebraska have been correlated with sunspot values (Bollinger 1934), and the latter bear a relation to precipitation (Stetson 1934). Rainfall in the seasons of growth influences the corn crop in South Africa (Scheepers 1938) and coffee yields in Hawaii (Dean 1939). However, no basis for long-range forecasts of crop successes, based on precipitation, could be found by Johnson (1940).

In the aquatic environment, effects of precipitation are more evident in streams than in lakes, because

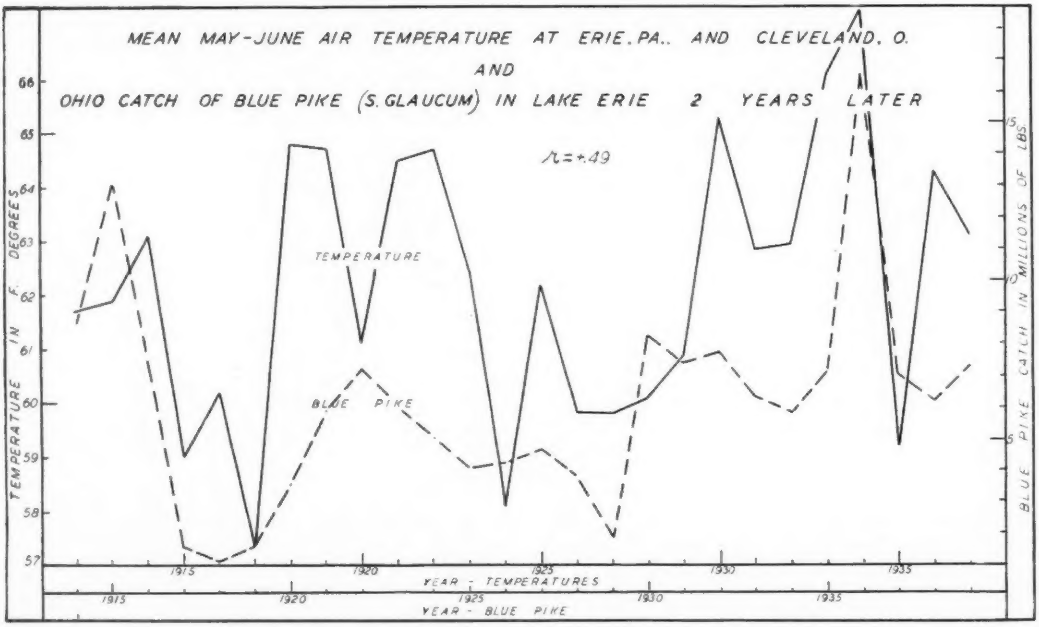

FIG. 9. Increases in average May-June air temperatures at Erie, Pa., and Cleveland, O., generally are followed by increased catches of blue pike *(S. v. glaucum)* two years later in the Ohio waters of Lake Erie.

the former react sooner and more violently to changes in precipitation than do the latter. Consequently, it is natural that there should have been more investigations of stream than of lake and ocean fishes, in relation to rainfall. Increased river flow, resulting from heavier precipitation, incites more activity on the part of Atlantic salmon to go upstream, and also facilitates their passage of barriers (Huntsman 1939). The period occupied for the main portion of each run of adult Pacific pink salmon to reach the spawning beds depends chiefly upon rainfall and freshet conditions (Pritchard 1937). Survival and movements of young salmon and trout are even more dependent on precipitation; dry summers restrict the habitat of large Atlantic salmon parr, and exposure of the parr to fish-eating birds reduces subsequent adult abundance (Huntsman 1938). Descent of Atlantic salmon smolts to the sea has been markedly accelerated by increased rainfall (White & Huntsman 1938), as has the extent of escapement of young Kamloops trout from tributary streams into Okanagan Lake (Clemens, Rawson & McHugh 1939). Snowfall, probably by maintaining stream flow as it melts, bears a positive correlation to the salmon catch in the Miomote River (Kubo 1938).

The sprat fishery of the west coast of Sweden decreases with dry summers and increases with wet seasons (Molander 1939). This variation is explained by hydrographic differences which affect the currents and influence the sprat movements.

Yellow pickerel.—The relationship between precipitation and yellow pickerel catch is one which could be inferred from previous considerations: (1), precipitation and turbidity are positively correlated, and (2), turbidity and pickerel catch are correlated negatively. As would be expected, precipitation and catch are inversely related. There is a statistically significant coefficient of correlation of —0.46 between the mean April-May precipitation at Toledo, Sandusky and Cleveland and the Ohio commercial catch of yellow pickerel in Lake Erie in the same year, from 1915 to 1936 (Fig. 10). Precipitations in the months of April and May individually are not significantly related to pickerel catches.

OTHER FACTORS

Investigators in the field of aquatic biology have discovered that many factors enter into the complex ecological relationships of fishes. Temperature, turbidity and precipitation have been touched upon in some of their relations to a few Lake Erie fishes; wind, light, food, currents and other physico-chemical conditions undoubtedly play parts whose importance in causing fluctuations in fish populations is as yet little known.

Broad differences in environment are evident in the different morphological forms assumed by European carp in different latitudes; the "Hungerform" is more common in Germany than in France (Wunder 1939). Latitudes and rates of growth show a connection in the European roach and bream (Vasnetsov 1934), in the golden shiner in Michigan (G. P. Cooper 1936), and in the smallmouth bass in Ontario (Doan 1940). The onset of spawning in the smallmouth bass occurs progressively later in the year from south to north (Langlois 1936a, Doan 1940).

The continuity of sunshine arriving at the sea has been correlated with subsequent plankton outbursts (L. H. N. Cooper 1934). There is excellent apparent correlation between May landings of mackerel by one fish company and the number of hours of bright sunshine during February and March of the same year (Allen 1910).

Submarine illumination has set up three zones of algal growth according to the light's penetration to different depths (Atkins 1939), and the results of absence of light needed by higher aquatic plants in turbid waters have been mentioned. Penetration of light into water has been studied in its government of vertical migrations of Crustacea (Waterman *et al.* 1939, Ullyot 1939), and of fishes ~~(Russell 1928)~~.

Changes in currents of the ocean are responsible

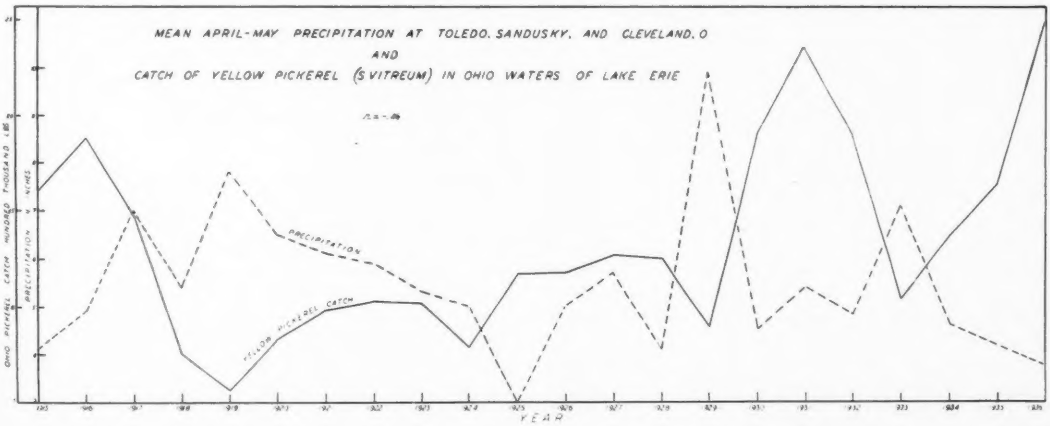

FIG. 10. The Ohio catch of yellow pickerel *(S. v. vitreum)* usually declines in years of high precipitation in the spring, and increases with dry weather.

for variations in the success of year classes and the consequent size of the commercial catch of salmon in the vicinity of the Tyne (Storrow 1932) and of haddock on Georges Bank (Walford 1938). Currents also affect catches of sprat (Molander 1939), and herring (Carruthers & Hodgson 1937), and affect the spawning migrations of salmon (Danilcenko 1936).

Variations in abundance of each year class of North Sea plaice showed a relationship to variations in atmospheric gradients of pressure in December-January of the year in which a year class was spawned (Carruthers 1937). Also, fluctuations in pressure distributions (Carruthers & Hodgson 1937).

Chemical conditions of the water may prove unfavorable to the survival of a year class of fishes, and thus affect population abundance. In an analogous instance, oyster larvae depend upon salinities above 20 parts per thousand in order to develop to the setting stage in Galveston Bay (Hopkins 1931). The lowering of Norris Reservoir in winter, and the inflow of cold water, resulted in surface waters of the lake characterized by low CO_2 tension and the lower waters with high CO_2; gizzard shad were unable to withstand the alterations and died in spite of a favorable O_2 content (Powers *et al.* 1939). There is no published evidence that chemical conditions in Lake Erie are much different from year to year, and no cause of fish fluctuations are expected from this source, except possibly in local situations such as Sandusky Bay.

It is difficult to attribute only mechanical action to certain factors some of whose components must certainly be chemical. Dannevig and Sivertsen (1933) have tested the influence of various physical factors upon cod larvae, and have shown that moderate light attracts, but that strong light kills the larvae. New larvae were at the most susceptible stage, and could also be killed when the pH was changed from 5.7 to 4.1. During gastrulation, the eggs of halibut, like those of cod, are very sensitive to mechanical influences (Rollefson 1935).

Lunar effects upon fishes have been recorded. On the second, third and fourth nights after a full moon, and after a new moon, spawning of Leuresthes attains its maxima (F. N. Clark 1926). Anglers' catches of rainbow trout in Paul Lake declined at periods of the full moon (Mottley 1938). However, off East Anglia there was a monthly rhythm in herring landings, with maxima which coincided with the periods of full moon; predictions of the success of the important autumn fishery were based in part upon whether or not there would be two or only one period of lunar fullness during a few critical weeks in October and November (Savage & Hodgson 1934).

Nearly all fishes in Lake Erie have depended upon plankton as an important part of their food at some time or other. The young of most species feed on plankton, and some continue to do so even as adults. Factors affecting the relationship between plankton and plankton-feeders must affect fish abundance also. Small artificial ponds fertilized for plankton production produced fish almost in direct proportion to the plankton crop (Smith & Swingle 1939). There was a slower growth of alewives in Kensico Reservoir than in Seneca Lake, New York, which may have been associated with chemical treatment of the water in Kensico to reduce plankton (Breder & Nigrelli 1936). It is not improbable that production of ciscoes in Lake Erie was directly dependent upon the amount of plankton Crustacea produced as food (Clemens & Bigelow 1922). However, in four South Moravian lakes the annual production of fish meat was not proportional to the amount of net plankton (Bayer & Bajkov 1929).

Various relationships have been found between fish catches and kinds and quantities of plankton in the water. A positive correlation between the quantity of zooplankton in the sea and English mackerel catches has been reported (Bullen 1910). Negative correlations between herring catches and the quantity of phytoplankton present in a given area (Henderson *et al.* 1936), and positive correlations between herring catches and the copepod Calanus (Hardy 1936) have enabled investigators to devise a plankton indicator, usable by commercial fishermen, which has a proven worth of being able to bring about a 24.5 ± 7.7 percent increase in the Scottish herring catch (Henderson 1936). Years marked by the presence of Channel water off Plymouth are characterized by a predominance of Sagitta and a scarcity of young fish (Russell 1936), and in these years there is also a low phosphate content of the water (Russell 1939).

Extraordinarily large numbers of young sockeye salmon have been thought to be responsible for an unusually early decline of the summer's supply of Entomostraca in certain years in Cultus Lake (Ricker 1937). Data are lacking regarding the possibility of similar plankton-fish relationships in Lake Erie.

RELATIONSHIPS BETWEEN FISHES

The relationships between fishes in Lake Erie involve competition for food and space. Differential reactions to environmental conditions may allow individuals of one species to survive, and comparable individuals of another species to succumb. It is probable that, under present conditions of fishing, there is little competition for space. Two individuals or groups may compete for the same food, or one may prey directly upon the other.

Intraspecific competition for food in years of large sockeye populations is sufficient to reduce the salmon's rate of growth in Cultus Lake (Ricker 1937). In 1929 young haddock were 37 times more abundant in the Skagerrak than they were in 1938, and in the latter year the fish were of a larger average size than when they were more abundant (Anderson 1938). Similarly, increased density of population decreased the growth of yellow perch in some Wisconsin lakes (Schneberger 1935), and food is of greater importance in the growth of lemon soles than are normal temperatures, salinity or depth of water (Rae 1939).

In May, 1934, pond Number 7 at the State Fish Farm at Akron, Ohio, was stocked with 60 adult bluegills; 150,000 young, weighing 115 pounds, were produced in that pond by October, according to Dr. T. H. Langlois. The following year the same pond received 120 adult bluegills, and that autumn the yield was 300,000 young with an aggregate weight of about 115 pounds. Therefore, this body of water could produce only a limited total weight of fish, and increases in numbers of individuals were accompanied by decreases in individual growth.

In a Coregonus fishery, Elster (1938) showed that individual growth rate was inversely proportional to the annual crop, so that in shallow ponds the maximum areal yield of fish was obtained at a population density which inhibited maximum individual growth.

In fishes which can avoid unfavorable circumstances there is a movement away from the source of distress, thus affecting fishing effort. Herring avoid jelly fish, squid, dogfish and whales, so that the presence of these affects the availability of herring (Lucas & Henderson 1936).

CISCO AND BLUE PIKE

The annual catch of ciscoes, Leucichthys, in Lake Erie has fluctuated violently. Until 1925 this species formed a large proportion of the commercial yield. It is claimed that in 1923 and 1924 the ciscoes congregated abnormally in the deep hole in the eastern part of the lake, where they were persecuted by gill netters and taken in amounts which indicated an unusually high apparent abundance (Van Oosten 1930). On resumption of normal distribution in 1925 the ciscoes were so scarce as to initiate the collapse of the industry dependent upon them.

"The history of the cisco is most interesting as it shows absolutely the relationship between the abundance of predatory and non-predatory fish in any given waters," says Schacht (1939), who draws attention to heavy catches of blue pike when ciscoes are scarce, and *vice versa*. He advances no evidence that blue pike feed on ciscoes, and gives no statistical treatment of the data from which he derived the correlation.

Total Lake Erie annual catches of ciscoes and blue pike are correlated with a statistically significant coefficient of —0.43 from 1913 to 1936. Correlation between the Ohio catches of these species is just at the 5 percent level of probability, from 1914 to 1939.

LAKE SHINER

Just as herbivorous rabbits and mice are links between carnivores and plants, so does the lake shiner, *Notropis atherinoides atherinoides* Rafinesque, constitute a "key industry" in the production of piscivorous pickerel, pike, saugers and bass in Lake Erie. Through the agency of these shiners planktonic organisms are converted into a form better utilizable by larger fishes. Plankton Crustacea formed two thirds of the volume of the contents of stomachs from lake shiners collected in Lake Erie in the summer (Ewers 1933). Diaptomus and Daphnia are the chief foods of these minnows taken at this laboratory in the winter.

Leach (1928) stated that the pike perches in Lake Erie eat mostly lake shiners the year round. About three quarters of the food of adult smallmouth bass in the western part of the lake is fish, and the most important food minnow is the lake shiner (Doan 1940).

Sixty-two yellow pickerel, 10 to 17 inches in length, taken in gill nets at Put-In-Bay in November and December, 1940, had eaten 82 percent lake shiners, 14 percent sheepshead, *Aplodinotus grunniens* Rafinesque, and 4 percent white bass, *Lepibema chrysops* Rafinesque, by volume. Thirty-nine saugers, 8 to 15 inches in total length, taken from Lake Erie simultaneously with the pickerel, were found to contain 27 percent lake shiners, 56 percent sheepshead and 17 percent of other fishes. Lake shiners are regarded as a pelagic fish, yellow pickerel are less restricted to the bottom than are saugers, and sheepshead live mostly near the bottom. Associations between pickerel and lake shiners, and between sauger and sheepshead are indicated in these food studies.

DISCUSSION AND CONCLUSIONS

Many of the factors affecting fishes in Lake Erie are probably little different from those operating in other of the Great Lakes. The most distinctive feature about Lake Erie, especially its western part, is the high turbidity of the water. High turbidity, coupled with a large area which becomes warm in summer, is the factor which most warrants discussion.

Further observations on the distribution of sauger bear a relation to the subject of turbidity. In the lower Scioto River drainage, Ohio, the catch in experimental nets has included a greater proportion of saugers than of yellow pickerel. The Scioto River is a lowland and muddy stream. In the Muskingum River, which is less turbid than the Scioto River, more yellow pickerel than saugers were obtained. According to Dr. C. M. Tarzwell, yellow pickerel are more numerous than sauger in Norris Reservoir in Tennessee, but sauger are commoner in the lower and more turbid reservoirs in Alabama.

It is interesting to speculate whether or not the water of western Lake Erie ever becomes so turbid that insufficient light for fish vision penetrates to the bottom. According to Clarke (1936), Lepomis can see at an illumination of 10^{-10} times the maximum value of daylight. To find the depth at which exists the minimum intensity of light for vision, the average number of meters of water which cause a reduction in light intensity of one logarithmic unit (to 10 percent) is multiplied by 10; throughout the period from September 5, 1939 to November 4, 1940, this depth varied from 0.4 to 6.4 meters (Chandler 1942). Therefore, vision for sunfish in western Lake Erie over this period would have been impossible beyond a depth of 4 meters when the water was most turbid, and beyond 64 meters when it was clearest. The

maximum depth of the western part of the lake is 12 meters.

The darkness at the bottom of Lake Erie during periods of increased turbidity probably affects various fishes differently. Individuals with small eyes can probably see less well than those with relatively large eyes, so that small-eyed fishes, or those with fewer retinal rods, might be at a greater disadvantage in hunting food by sight in dim light than others. Catfishes are provided with sensitive barbels, and sturgeon make considerable use of their tactile senses. During high turbidities it is possible that in order to obtain food some fishes would be forced to approach the surface in order to receive sufficient light by which to see their prey; here, they might receive increased advantage by finding a concentration of smaller food fishes also attracted upward by the concentration of plankton nearer the surface in the turbid water, or they might be at a disadvantage due to unfavorable thermal or chemical conditions prevailing in the upper waters.

Ciscoes, whitefish, blue pike and lawyer, *Lota lota maculosa* (Le Sueur), are regarded as fish of the colder and, in summer, deeper waters of Lake Erie. Most other species live in the warmer parts of the lake. A warm spring, as measured by water temperatures in April and May, would probably allow fishing to commence at an early date and an increased total catch would result. Also, a warm spring would probably stimulate the warm-water fishes to greater activity and increase their chances of being taken by fishing gear. There is a significant r of $+0.48$ between the April-May water temperatures at Erie, Pa., and the total Ohio catches (exclusive of whitefish, ciscoes and blue pike) in the same year, from 1918 to 1938. Lawyer, catches of which have amounted to about one third of a million pounds annually for the past few years, have of necessity been included with the warm-water fishes because no records for this species are available between 1918 and 1935 (Wickliff 1939). Therefore, higher temperatures in the spring are associated with heavier catches of warm-water fishes in Lake Erie.

In Lake Erie, the cisco, whitefish, lake trout, *Cristivomer namaycush namaycush* (Walbaum), yellow perch, yellow pickerel, blue pike, sauger, and lawyer approach the southern limit of their range in eastern North America. It may be assumed that northward the waters in which they are found become, on the average, colder. Therefore, in Lake Erie the factor to which these fishes react most strongly should be temperature; they seek colder water in the summer by going deeper. Movements of tagged blue pike and yellow pickerel in Lake Erie support this view; the former inhabit the colder water, and the latter are more tolerant of warmer water but still move eastward out of the excessively high temperatures in the summer in the western portion of the lake.

Bass, channel catfish, carp, *Cyprinus carpio* Linnaeus, and sheepshead are, in Lake Erie, in about the middle to northern parts of their range, and should react to temperatures by keeping in the warmer parts of the lake. Tagging returns for these fish are few, but support this hypothesis, since these species maintain their centers of movement and abundance in western Lake Erie.

The present study is the first to seek quantitative relationships between abundance of fish in Lake Erie and some of the meteorological and limnological conditions of the environment. Turbidity and temperature have been found to be of considerable importance. Distinct effects of each upon certain species have been demonstrated, but the actual mechanics of the operation of these factors are largely unknown. It may be that variations in natural factors are of greater importance as modifiers of fish abundance than are changes in the artificial manipulation of the population by commercial fishing.

SUMMARY

By methods of correlation, a survey has been made of some of the factors concerned in the abundance of Lake Erie fishes. The salient features of the results of the study may be listed as follows:

1. Average air temperatures at several stations along the south shore of Lake Erie vary similarly, and the mean temperatures decrease in order from the southwest to northeast.
2. Changes in average water temperatures are both general and in the same direction throughout most of Lake Erie, and are positively related to air temperatures.
3. Mean precipitation varies similarly along Lake Erie, as does turbidity, and the latter decreases in value eastward. Turbidity of the lake water depends in part upon the amount of precipitation along the shore.
4. Increased turbidity results in a higher proportion of zooplankters near the surface than at greater depths.
5. A return of 2.2 percent has been obtained from 3,761 tagged fish. Recoveries of tagged blue pike show this species' restriction to the colder waters of Lake Erie, but yellow pickerel are more tolerant of warmer waters.
6. Higher average temperatures in April and May were followed by increased catches of warm-water fishes in that year, and of the total Ohio catch one year later, but had no demonstrable effect on catches of perch, pickerel, and sauger individually. High temperatures in May and June resulted in heavier catches of blue pike two years later.
7. Increased spring turbidities were associated with lower total Ohio catches in the same year, had no direct effect on the perch fishing, but were followed by increased sauger catches three years later.
8. Light catches of yellow pickerel were made in years of high precipitation in the spring.
9. Total Lake Erie catches of ciscoes and blue pike were negatively correlated.
10. The lake shiner is one of the most important food organisms in the lake, and constituted 82 and 27

percent of the food of samples of yellow pickerel and sauger, respectively, in western Lake Erie.

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HERBACEOUS VEGETATION A FACTOR IN NATURAL REGENERATION OF PONDEROSA PINE IN THE SOUTHWEST*

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McB

* Abnormal cost of illustrations borne by author.

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HERBACEOUS VEGETATION A FACTOR IN NATURAL REGENERATION OF PONDEROSA PINE IN THE SOUTHWEST

INTRODUCTION

Subordinate vegetation, commonly called ground cover, plays an important role in the life of forests. Not only does it exert a direct influence upon soil and trees but its character may be an indicator of soil and moisture conditions. There are two broad types of ground cover—herbs and shrubs. Herbs, particularly the grasses, tend to prevail on the heavier soils and shrubs on the lighter, more porous soils. Grasses have a relatively shallow and compact root system adapted to intensive feeding in superficial soil layers. Shrubs as well as trees prefer the more open soils which permit deep root development and deep moisture penetration. Shallow-rooted herbs are dependent on summer showers, whereas the deeper rooted shrubs and trees are able to grow with little or no summer precipitation if the soil is well saturated during the winter months.

Grass is the prevailing type of ground cover in the pine forests of the Southwest. A pronounced midsummer rainy season as well as relatively heavy soil favors the grasses. In this region pine seldom germinates at any other time than during the summer rainy season, because the spring is usually either too cold or too dry. Copious summer rains are essential to early survival as well as germination; if the rains are deficient the young seedlings are at a disadvantage in competing with older vegetation. Grass roots commonly form a dense network in the upper 6 inches of soil, and a few go deeper (Fig. 1). Pine seedlings have some superficial roots which, however, are no match for the grass roots in dry periods. At such times, unless the pines have pushed their taproots below the intensive layer of grass roots, they perish.

Some grasses offer keener root competition than others, depending on their growth habits. Up to June 1 soil moisture is usually adequate but the temperature is too low for vigorous growth of most plants, including the pines. By the middle of June temperatures begin to attain effective intensity but soil moisture becomes limiting for shallow-rooted vegetation. Two of the most common grasses, mountain muhly *(Muhlenbergia montana)* and blue grama *(Bouteloua gracilis)*, grow but little until the arrival of the July rains, unless much more than the occasional light showers fall in May and June. Several other species, conspicuous among which is the aggressive bunchgrass, Arizona fescue *(Festuca arizonica)*, normally begin vigorous growth in May and continue until they have exhausted the available moisture in the upper foot of soil. These relations suggest an explanation for the observation that pine reproduces better on sites occupied mainly by muhly or grama grass than on sites where fescue predominates.

The widespread experience of foresters that tree seedlings are adversely affected by competing vegetation has been confirmed experimentally by Clements, Weaver, and Hanson working in the prairies of the Middle West and by Pessin in the longleaf pine belt of Louisiana. In the light of age-long experience in agriculture, explanation may seem superfluous. No farmer would plant corn in a grass sod, nor would a nurseryman attempt to grow trees from seed without cultivation and weeding. But in extensive forestry practice a delicate pine seedling is expected to compete successfully with whatever vegetation has prior possession of the soil.

A different picture is painted by soil conservationists and those who stress forage production. They point to the benefits of ground cover in stabilizing soil and promoting infiltration of water. They maintain that an improved soil condition resulting from the presence of a protective soil cover more than offsets any temporary adverse effect of root competition. A common viewpoint is that grass by shading the soil conserves surface moisture essential to germination of seeds lying uncovered or but lightly covered by soil. There is a widespread belief that pine seedlings require partial shade and winter protection until they are several years old.

The foregoing viewpoints are in turn subject to modification by other considerations. It is true that anything which retards evaporation from the surface of the soil favors the germination of seeds; but it is also true that germination is but the initial chapter and not the most critical one in the early life of a tree. As for surface run-off, suffice it to say that pine lands in the Southwest are for the most part comparatively level and that the moisture supply on which trees depend mainly is derived from snow which normally melts slowly and filters into the soil without the aid of retarding agents other than forest litter. Infiltration capacity in granitic soils on 10 percent slopes in Colorado has been found by Johnson and Niederhof to increase significantly under a cover of mountain muhly but not under a cover of Arizona fescue, when compared with bare soil on the same site. In relation to regeneration, a forester thinks of vegetation control as only a temporary measure, knowing that once a full stand of trees becomes established a supreme soil cover is in the making.

Notwithstanding a preponderance of evidence in this country and abroad pointing to competing vegetation as a handicap to successful forest regeneration, there are two sides to the question. Ground cover plays a useful role, within limits, and pine seedlings do gain a foothold in spite of a dominating grass cover, under certain conditions. What these conditions and limitations are and what can be done

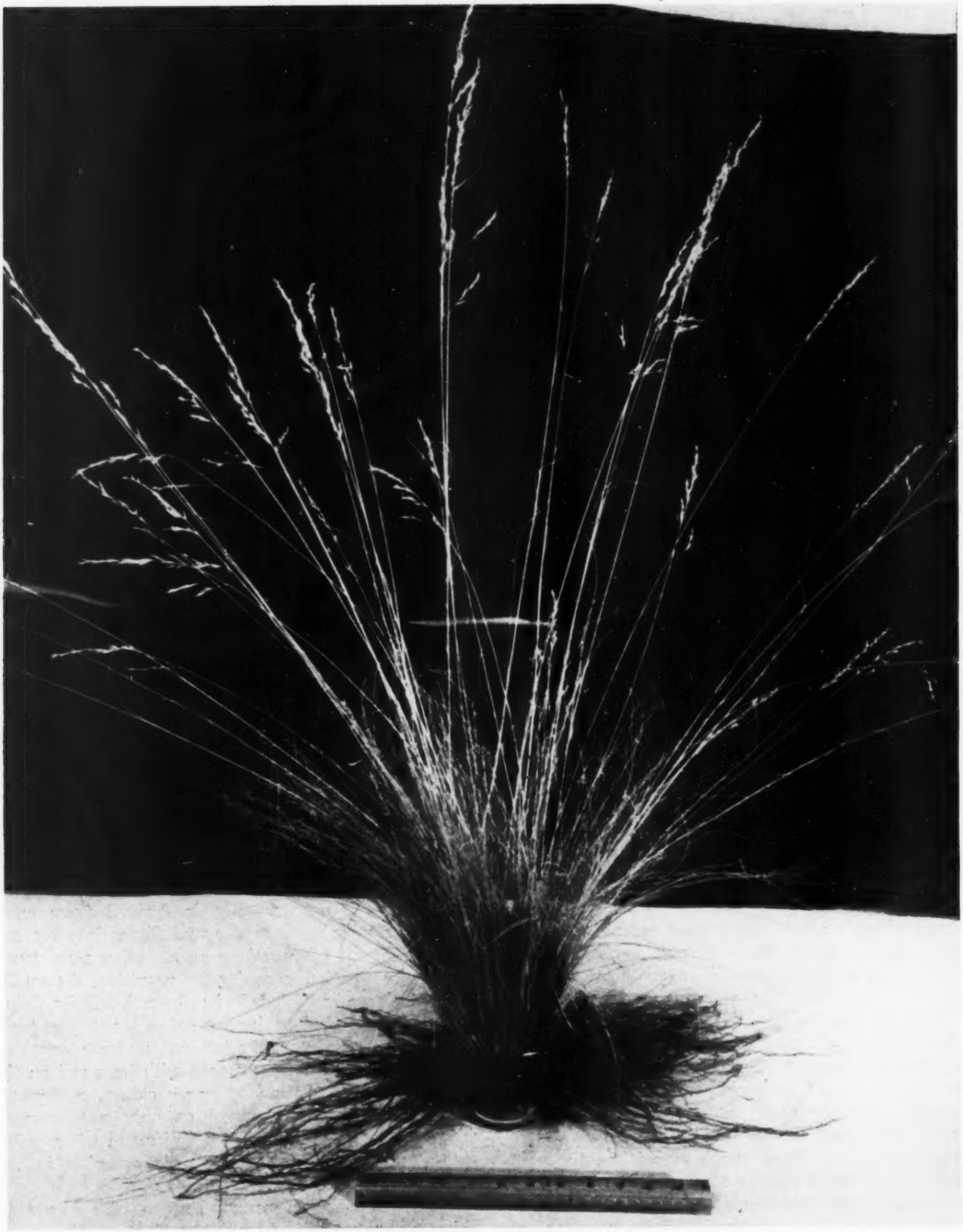


FIG. 1. An individual plant of Arizona fescue. The roots radiate in a thin, dense layer confined largely to the upper 6 inches of soil. A few deep roots enable the plant to grow through prolonged dry periods. The superficial roots offer intense competition to young pines. The flat conformation of the root system is natural, but the spread is wider than indicated by photo (scale is 12 inches long).

to mitigate adverse influences is the subject of this study.

OBSERVATIONAL RECORDS

Studies of natural reproduction of ponderosa pine from 1908 to the present time have continually focused attention on the influence of soil, moisture, root competition, litter, and shade. Early observations attached much importance to shade and shelter, but record plots over a period of 10 years gave negative results because there was little survival anywhere. Moreover, the picture was generally obscured by the dominating influence of browsing by livestock.

In 1919 came the first opportunity to study the

A

B

FIG. 2. Luxuriant vegetation grows around stumps after litter has decayed. *A*, Pine seedlings 5 years old and 2 feet tall in a stump group where grazing has held herbaceous vegetation in check. *B*, Stump group on area closed to grazing. Many pine seedlings started but died; clumps of seedlings in distance occur where grass is less luxuriant.

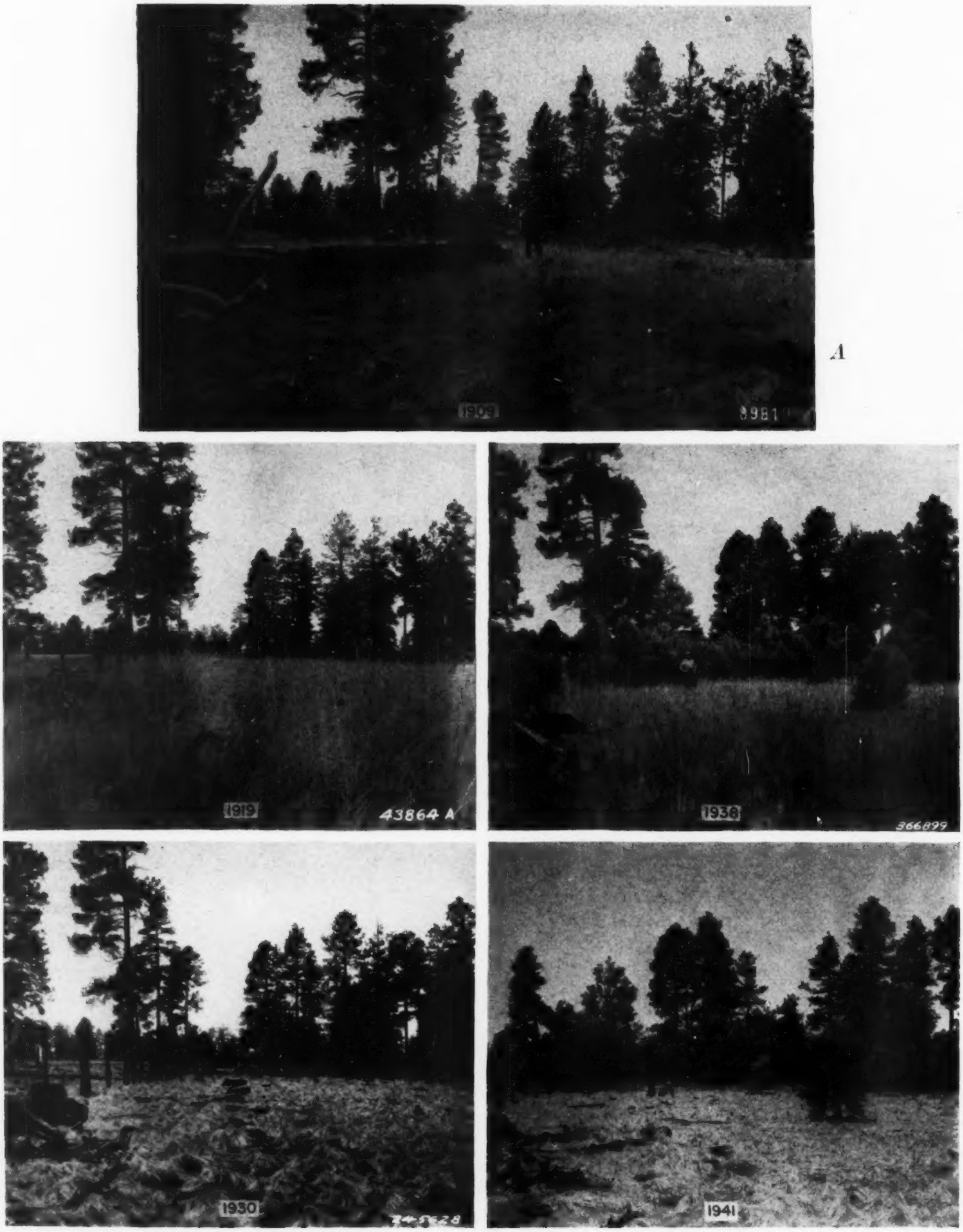


FIGURE 3

Two series of photographs from the same point at 10-year intervals from 1909 to 1941. Photos in 1909 directly after logging; those of 1941 after a second logging 30 years later. Area closed to grazing througout the entire period. *A*, Arizona fescue promptly took possession. Many pine seedlings started in 1919, but died within a year.

B

FIGURE 3 (continued)

Where pine saplings appear in the distance (1938 and 1941 photos) the grass is predominantly muhly. *B*, Arizona fescue predominates on left side, adjoining *A*; on right muhly predominates. The two grasses are readily distinguishable, in the 1909 and 1930 photos, by the lighter color of fescue.

behavior of seedlings in adequate numbers over a wide range of conditions. More than 100 seedling plots were followed through from 1919 to 1930. The findings, covering the whole field of natural reproduction, have been presented in a series of publications whose highlights bearing on the present subject are briefly summarized in the following paragraphs.

Under tall grass or weeds, germination was generally good but survival and growth poor.

On moderately or closely grazed areas, survival was better unless browsing was too severe, but growth was slow.

On denuded spots, such as log landings and roads, germination was sometimes deficient because of high evaporation or because the seeds were swept away by water; but where seedlings occurred they grew more rapidly than where obliged to compete with herbaceous vegetation.

Deep cultivation on 5 x 10-foot plots acted unfavorably, probably because it brought clay to the surface; moreover, denuding small plots was found to remove root competition only temporarily because the soil was invaded by roots from surrounding plants.

In the shade and litter under tree groups seedlings were at first more abundant than elsewhere, but subsequent mortality was also highest and it took place under circumstances which pointed to deficient insolation rather than deficient moisture. Soil samples during critical drought periods showed more moisture in shaded situations than beyond the shade influence of the trees.

Both survival and growth excelled on the littered areas around stumps where tree roots had ceased to be active, and where herbaceous vegetation had not yet entered; soil moisture was found to be much more abundant in these situations than where herbaceous vegetation was present.

Three years after germination, pine seedlings around stumps were 6 to 9 inches tall while those in grass-covered, grazed areas were only 2 to 3 inches tall and those which started in dense bunchgrass had become virtually extinct. Seedlings on log landings, roads, and other areas denuded and without litter were generally intermediate in size.

Photographic records supplement the foregoing observations. Figure 2*A* shows the characteristic grouping of vigorous seedlings among stumps in 1924, 5 years after germination. In this instance germination took place 6 years after logging, and before herbaceous vegetation had invaded the space left vacant by removal of the trees. Another area on which abundant germination followed logging by 10 years, and on which herbaceous vegetation had taken full possession in the meantime was a complete failure as shown in Figure 2*B*.

In Figure 3, repeated views from fixed points at decade intervals through 32 years from 1909 to 1941 show the progress of pine reproduction in two types of grass within a fenced area closed to grazing. The camera fields in the two series were almost side by side in a large opening. Both 1909 photographs were taken a month after logging. In Figure 3*A* the main portion of the opening was dominated by Arizona fescue *(Festuca arizonica)*; in Figure 3*B* the left side (adjoining 3*A*) was fescue but on the right was a sparse stand of muhly *(Muhlenbergia montana)*. The two species may be distinguished in the 1930 photographs (taken in early spring) by the lighter color and matted appearance of fescue. In series *B* the transition between muhly and fescue follows closely an imaginary line from the camera point to the stump. As early as 1925 seedlings became conspicuous in the muhly association, as seen on the right-hand side of B. Several 5 x 20-foot plots on the fescue side in 1919 revealed numerous seedlings, nearly all of which died during the ensuing winter and dry June period of 1920. The 1938 photographs show a full stand on the muhly side and only occasional survivals in the fescue. A similar transition from fescue to muhly, accompanied by increasing density of seedlings, occurs in the distant border of the opening as seen in *A*.

Figure 3*A* is typical of ungrazed fescue sites, Figure 4 of grazed sites. The 1909 photograph in Figure 4 indicates that only about half of the grass cover is fescue, other species being mostly muhly and beardless bunch *(Blepharoneuron tricholepis)*. Grazing was moderate to heavy from 1909 to 1925, light after 1925. The final result in this series indicates that grass competition could not have interfered seriously with the pine seedlings, and by comparison with Figure 3 leads to the inference that grazing may be beneficial. This view is typical of extensive areas on which the bunchgrasses were rather closely grazed.

A question which naturally arises is whether the observed differences in pine reproduction as related to fescue and muhly are attributable to direct influences of the grass or to soil differences which might account for the kind of grass as well as the ability of pine seedlings to become established. This, among other questions, receives attention in the experiments described in the following pages.

EXPERIMENTAL DATA

In order to check the earlier findings under controlled conditions and evaluate the various factors, tests were begun in 1928 and have been carried on to the present time. The general plan has been to sow equal quantities of pine seed or to plant nursery-grown stock on plots representing different conditions of grass cover, within exclosures against livestock and rodents. Sowings were made in 1928, 1929, 1937, and 1938, and plantings in 1937 and 1938. The 1928 sowing was a complete failure because summer rains were not properly distributed for germination. In 1938 germination was light and subsequent dry summers resulted in such high mortality on all plots as to render comparisons of little significance. Both plantings were successful. Conclusions are therefore based primarily on the sowings of 1929 and 1937 and upon the plantings of 1937 and 1938.

FIG. 4. A series of photographs from the same point, 1909 to 1941. The grass is a mixed stand of fescue and muhly moderately grazed. The 1909 photo was taken directly after logging, the 1941 photo after a second logging 30 years later. (Camera elevated 8 feet above ground in 1941 photo.)

A

B

FIGURE 5

Series of grass plots variously treated, all seeded to ponderosa pine in 1929 and all within rodent exclosure. *A*, General view in 1936, plots in receding order: (1) Grass undisturbed (immediate foreground, only part of plot visible); (2) clipped to height of 6 inches; (3) clipped to height of 2 inches (stake in path between 2 and

C

D

FIGURE 5 (continued)

3); (4) denuded and weeded (dense stand). *B,* Photo in 1941. Left of path denuded plot; right, grass clipped to 2 inches. *C,* Photo in 1941. Left of path, grass clipped to 2 inches, right clipped to 6 inches. *D,* Photo in 1941. Left of path, grass clipped to 6 inches, right no clipping.

Precipitation records during the growing seasons from 1928 to 1941, inclusive, as given in Table 1 go far toward explaining failures and successes. As has been stated, germination almost invariably takes place in July or August, although it may be delayed until early September. Only in one year, 1919, has appreciable germination occurred earlier than July 1. Summer records on the experimental area (Table 2) vary considerably from those at Fort Valley for current months, partly because readings on the experimental area were made only at weekly intervals. Annual totals probably are in close agreement.

TABLE 1. Monthly precipitation at Fort Valley, 6 miles from the experimental plots, 1928 to 1941.

Year	Precipitation – inches												
	January	February	March	April	May	June	July	August	September	October	November	December	Annual
1928	1.07	1.94	0.80	0.58	1.12	0.10	1.95	5.78	0.44	3.07	2.28	2.02	21.15
1929	3.24	2.50	2.14	0.97	0.84	T	4.88	7.24	1.88	0.40	0.03	0.01	24.13
1930	4.18	1.87	2.27	1.26	1.08	0.55	7.32	2.22	1.64	0.28	2.84	0.05	25.56
1931	0.46	2.76	0.28	1.57	1.07	1.63	2.48	4.64	2.67	1.05	3.07	3.22	24.90
1932	1.42	6.19	1.13	1.50	0.65	0.56	2.04	3.79	1.47	1.60	0.00	2.65	23.00
1933	3.17	0.59	0.06	1.60	1.08	0.14	2.84	4.05	1.25	2.97	1.26	1.09	20.10
1934	0.77	1.28	0.49	2.90	1.55	0.40	1.88	5.92	0.30	0.08	1.15	1.38	18.10
1935	4.70	2.75	2.90	1.10	0.91	0.12	2.14	4.78	2.83	0.09	0.85	1.26	24.43
1936	0.31	4.52	2.71	0.41	0.20	1.66	5.42	5.87	1.89	1.79	0.58	3.13	28.49
1937	4.63	4.50	3.92	0.25	1.63	1.62	4.40	2.19	1.87	0.00	0.25	2.98	28.24
1938	1.48	3.94	5.63	0.76	0.16	1.27	1.34	4.26	1.16	0.95	0.72	3.38	25.05
1939	2.08	2.09	1.34	1.05	0.06	0.04	0.63	3.97	3.66	0.55	1.47	0.14	17.08
1940	2.90	3.37	0.41	2.98	0.30	1.37	0.13	2.30	5.47	3.67	1.59	4.35	28.84
1941	2.56	2.74	3.09	4.48	0.64	0.98	1.87	1.87	3.30	4.93	1.08	3.72	31.26

TABLE 2. Monthly precipitation, May to October, near the experimental plots, 1937 to 1941.

Year	Precipitation – inches					
	May	June	July	August	September	October
1937....	0.83	1.60	5.63	3.55	0.11	1.37
1938....	0.22	—	3.47	3.09	2.99	0.17
1939....	0.15	—	0.71	2.83	7.47	0.57
1940....	0.12	1.53	0.89	3.34	4.15	4.39
1941....	0.19	0.82	1.24	1.57	2.94	5.42

1929 SEEDING EXPERIMENT

Pine seed was sown on 1 x 3-meter plots within an area of fescue undisturbed by grazing since 1910. Grass treatments and arrangement of plots were as shown in Table 3. Plots were separated by paths 2 feet wide. These same plots were seeded in 1928 but, as previously stated, germination failed. Probably some of the 1928 seed remained dormant and germinated in 1929, along with the seed sown in 1929, which may in part explain the unequal numbers of seedlings recorded in August 1929. However, this variation appears to be unimportant inasmuch as all plots were adequately stocked in 1929, and ultimate survival was unrelated to initial numbers.

Table 3 reveals interesting facts as to sparsity of grass cover as measured near the ground line. What is usually characterized as a dense stand of bunchgrass actually occupies but little more than one tenth of the ground surface. As the grasses grow to a height of 2 feet or more, however, the spreading leaves and flower stalks of neighboring grass clumps tend to merge and form a fairly close canopy. But when the leaves and stems are clipped or eaten off close to the ground, large bare spaces become apparent. A normal reaction to such disturbance is the spontaneous appearance of weeds whose seeds are ever present and await only moisture and sunlight to assert themselves.

TABLE 3. Density of perennial grasses on the plots at the beginning of the experiment, as determined by charting in 1928.

Treatment of grass	Plot No.	Density[1]		
		Fescue	Others	Total
Natural, no clipping....	1	0.0823	0.0033	0.0856
Clipped to 10 inches ...	2	.0765	.0277	.1042
Burned in 1928........	3	.1259	.0376	.1635
Denuded in 1928......	4	.....	.....	.....
Clipped to 2 inches....	5	.1681	.0226	.1907
Clipped to 6 inches....	6	.1070	.0083	.1153
Natural, no clipping....	7	.1002	.0032	.1034

[1]Assuming complete cover = 1. Measurements 1 inch above ground.

A preliminary paper published in 1934 has presented the findings through the year 1933. They are briefly as follows: By far the best survival and growth of pine seedlings were obtained where grass and all other competing vegetation were completely removed and kept out by weeding. Results were noticeably improved where the grass was clipped twice annually to heights of 2 and 6 inches, as compared with undisturbed grass, and the 2-inch clipping plot was superior to the one clipped to 6 inches. Soil moisture determinations showed a decisive margin in favor of the denuded plot during the June-July drought period.

Survival and height growth from 1929 to 1941, inclusive, are shown in Table 4, and a visual comparison of the several plots may be obtained from Figure 5. Mortality practically ceased after 1932. The decline in numbers on the denuded plot is due to artificial thinnings in order to prevent stagnation; growth on this plot is probably still being retarded by intense competition between the trees themselves, the largest of which are now over 6 feet tall. The trees on all the grassy plots have recently increased their growth rate, evidently because the survivors now overtop the grass and have established root systems which make them more or less independent of moisture in the superficial soil strata.

The comparatively good results on the plot on which the grass was burned before seeding are not explained. Whether the chemical composition of the soil was affected by the ash is not known because no analyses were made. The burning took place in 1928 and was not repeated before the 1929 seeding. After

TABLE 4. Record of germination and survival of ponderosa pine seedlings on seven grass plots treated in different ways, pine seed sown in 1929.

Treatment of grass	Plot	Number of live seedlings on different dates: 1929 August	1929 November	1930 May	1930 August	1931	1932	1933	1941	Height of seedlings: 1933 Above 6 in.	1933 Above 10 in.	1941 Above 40 in.	1941 Above 60 in.	1941 Above 80 in.	1941 Av. dom.
										No.	No.	No.	No.	No.	In.
Natural, no clipping....	1	309	151	28	6	1	1	1	1	0	0	0	0	0	20
Clipped to 10 inches.....	2	169	91	43	1	0	0	Denuded in 1932							
Burned in 1928......	3	332	271	91	23	15	10	8	8	0	0	1	0	0	26
Denuded in 1928......	4	382	374	288	148	109	100	71	*18	69	29	18	14	5	60
Clipped to 2 inches.....	5	258	219	116	30	0	11	11	10	2	1	7	3	0	42
Clipped to 6 inches.....	6	241	218	56	8	5	4	4	4	2	1	2	1	0	36
Natural, no clipping....	7	90	81	20	11	8	5	5	5	1	0	1	0	0	30

*Thinned in order to prevent destructive competition.

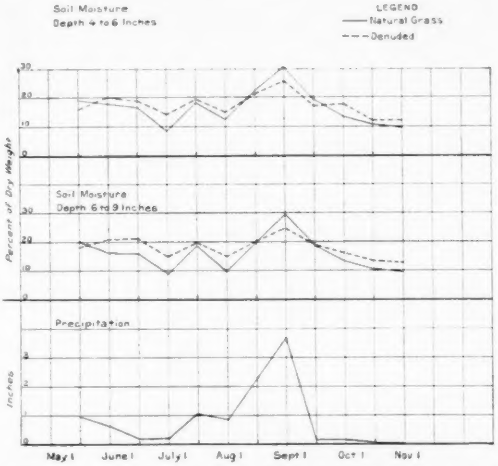


FIG. 6. Soil moisture and precipitation in natural grass cover and on denuded plots, 1934.

the first year the grass cover was indistinguishable from that of the two natural plots.

The last remaining seedling on the 10-inch clipping plot died in 1931. Whether the complete failure of this plot is related to clipping is not known. Except for absence of seed stalks the plot appeared little different from the unclipped plots because clipping removed few of the leaves. Since there were no more seedlings to record, the plot was denuded in 1932. After denuding, small sections of the plot were resown in 1932 and 1937; both of these sowings produced dense stands of seedlings, similar to that of the original denuded plot. The major portion of the plot was used for soil sampling to represent denuded areas, because the original denuded plot had become densely stocked with seedlings.

Soil moisture determinations presented in the previous paper were repeated in 1934; the results are given in Table 5 and Figure 6. Samples were taken at depths of 4 to 6 inches and 6 to 9 inches at 15-day intervals from May 15 to November 1. The 4- to 6-inch samples are considered as representing the layer of most intensive root activity on the part of the grasses and of small pine seedlings. The surface soil to a depth of one half inch is most concerned in germination, but germination is usually less of a problem than subsequent survival. Previous tests have shown that surface moisture fluctuates greatly and that almost daily showers over a period of 3 to 4 weeks are necessary for germination. The 6- to 9-inch layer, though containing fewer grass roots than the 4- to 6-inch layer, is penetrated by deep-rooted forbs and is on the whole well occupied. At about 9 inches the loamy top soil on this area gives way to a more clayey subsoil.

As in the 1933 moisture determinations, the denuded plot maintained a substantial margin over the grassy plots during the dry period of late June and early July. Although the wilting coefficient was not determined for these samples, previous determinations in this immediate vicinity gave values of 12 to 14 percent for the upper 6 inches of soil. Thus, it is apparent that the grassy plots must have been under severe stress not only during the June-July drought but also during secondary droughts later in the season. In all of these dry periods, except possibly at the close of the season, the denuded plot appears to have maintained a safe margin. It is well to repeat that the denuded plot on which the soil samples were taken is not the original denuded plot which at the time of these soil samplings had become densely

TABLE 5. Soil moisture in percent of dry weight at depths of 4 to 6 and 6 to 9 inches, at 15-day intervals from May 15 to November 1, 1934.

Treatment of grass	Moisture in soil on different dates: May 15	June 1	June 15	July 1	July 15	August 1	August 15	September 1	September 15	October 1	October 15	November 1
	%	%	%	%	%	%	%	%	%	%	%	%
	Samples at depth of 4 to 6 inches below surface											
Natural..........	17.7	15.2	15.1	7.8	18.8	13.1	22.0	30.7	20.0	13.9	10.8	9.7
Denuded 1932...	16.1	20.2	18.9	14.1	19.4	15.0	20.9	26.1	17.0	17.8	12.2	12.2
Burned 1928.....	17.3	14.6	11.5	8.5	16.5	17.7	24.4	26.6	18.3	14.5	8.9	8.2
Denuded 1928...	No samples											
Clipped to 2 in...	18.1	16.6	18.4	7.9	17.5	15.3	26.4	28.7	19.2	16.6	11.7	11.1
Clipped to 6 in...	18.9	15.8	16.1	8.3	17.2	20.0	21.9	24.3	19.5	15.2	11.7	11.1
Natural..........	20.4	20.2	17.6	9.6	18.5	12.1	22.9	30.8	18.5	12.7	9.8	9.8
	Samples at depth of 6 to 9 inches below surface											
Natural..........	19.3	14.4	15.3	8.0	19.3	9.5	19.5	30.2	19.0	13.7	10.6	9.9
Denuded 1932...	17.9	20.5	21.0	14.6	19.4	14.7	19.6	24.4	18.3	16.0	13.3	12.7
Burned 1928.....	17.3	13.4	13.0	8.4	15.6	16.5	25.0	26.2	18.2	14.3	8.6	8.3
Denuded 1928...	No samples											
Clipped to 2 in...	18.2	15.5	19.1	8.4	17.0	12.3	24.6	26.9	19.2	16.5	11.7	11.3
Clipped to 6 in...	18.2	14.3	17.2	8.3	16.7	17.4	21.1	25.8	19.3	14.8	11.8	11.7
Natural..........	19.7	18.5	16.9	10.1	18.0	10.7	20.2	28.3	18.5	12.9	10.0	9.7

stocked with pine seedlings. Moisture determinations among these seedlings would have been interesting but were not made because of the soil and root disturbance that would have resulted. A low temperature of 18° F. on September 26 checked the activity of nearly all herbaceous vegetation. It is improbable that root competition was much of a factor during the month of October. Experiments with pines in sealed pots have demonstrated that in a dormant state they can persist for months in soil whose moisture content is practically at the wilting point.

Contrary to expectations, clipping even as short as 2 inches twice annually did not seriously affect the cover. Arizona fescue, after 10 years of clipping twice annually, had given way almost entirely to muhly, beardless bunch *(Blepharoneuron tricholepis)*, and forbs where clipped to 2 inches but less completely where clipped to 6 inches (Fig. 7). Muhly and beardless bunch have thrived under 6-inch clipping. After the 10th year, clipping was curtailed to once annually—at the close of the growing season. Muhly appears to be capable of holding its own under this program, even when clipped as short as 2 inches.

A parallel series of plots outside the rodent exclosure was discontinued in 1934 because, rodents having destroyed nearly all seedlings in the first years, there was no further object in seedling records. An examination of the grasses in the fall of 1937 indicated no apparent deterioration of Arizona fescue during the 5 years when clippings were made 2 or 3 times each summer. At that time, however, the contrast with corresponding plots clipped continuously during 10 years was very marked.

1937 Seeding Experiment

For the purpose of checking results of the 1929 experiment on a different site and in a different period, a new series of plots was seeded in 1937. An area 100 feet square, clear of trees and dominated by Arizona fescue, was enclosed with a rodent-proof fence. Like the area selected in 1928, it was a "fail spot" surrounded by areas which had restocked to pine in 1919 (Fig. 8). Although fescue was dominant, muhly was an important component of the grass association. The plots were 8 feet square in two ranks separated by a path 2 feet wide. Two plots represented each of the following treatments: (1) natural, undisturbed grass, (2) clipped to 4 inches twice annually, (3) denuded and weeded, (4) denuded but not weeded. In order to insure uniform opportunities for germination, the pine seeds were planted in "hills" of 2 or 3 seeds each, 100 hills to the plot. On the grassy plots, hills were planted in different positions with reference to the tufts—in edges, in dead middles, and in bare spots between tufts.

The purpose of the paths was to facilitate examination rather than to provide isolation strips. Although isolation strips would have been desirable, the idea was abandoned because of the small size of continuous areas of uniform grass cover. The dimensions of the 1937 plots were increased to 8 x 8 feet in order to permit studying border effects. Such effects were noticeable only in the case of denuded plots which clearly showed the influence of root action by plants in the paths and on adjacent plots.

Table 6 gives a 5-year record of survival and

TABLE 6. Survival and height growth of pine seedlings grown from seed under different treatments of herbaceous vegetation. 1937 seeding.

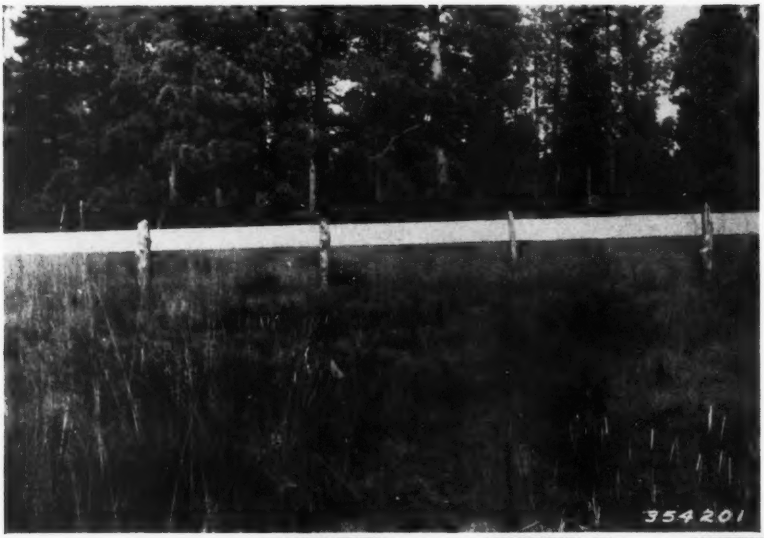
Plot No.	Treatment	Number of hills on different dates					Height of seedlings September 1941		
		August 1937	May 1938	October 1938	May 1940	May[1] 1941	Above 6 in.	Above 10 in.	Average dominant
							No.	No.	In.
1......	Denuded—weeded.........	100	64	47	40	35	27	13	12.1
2......	Natural Sparse grass....	81	47	15	11	6	0	0	[2]4.2
3......	Denuded—not weeded.....	97	76	34	17	12	0	0	5.3
4......	Clipped to 4 inches........	77	55	20	13	9	0	0	3.1
5......	Natural Dense grass.....	57	41	11	6	1	0	0	3.3
6......	Denuded—not weeded.....	86	65	27	11	8	0	0	4.5
7......	Clipped to 4 inches........	64	33	6	2	2	0	0	2.4
8......	Denuded—weeded.........	81	57	46	41	39	22	12	11.6

[1]All hills reduced to 1 seedling May 1941.
[2]All dominants are in open spaces.

growth, and Figure 9 presents a picture of typical plots in 1941. It is obvious that denuding and weeding brought what was essentially a repetition of results obtained with similar treatments in the 1929 seeding. Where denuding was not followed by weeding, muhly, almost to the exclusion of fescue, came back through root growth and in 2 years had formed a complete stand. Pine survival and growth on these plots was noticeably below that on the denuded and weeded plots, but better than on the clipped or natural plots. Clipping the grasses has undoubtedly aided survival, though to a less extent than denudation. One of the natural plots contains several seedlings which promise to survive. This plot has a less dense stand of grass than its companion; all of the seedlings are directly in or in the edge of open spaces 15 to 20 inches in diameter.

Soil moisture determinations were made only in 1938 and 1941, and then only in what was judged to be the height of the dry season. The results repeat the story of the 1929 experiment. Early in July, before the summer rains began, the denuded and weeded plots showed a margin of 4 to 5 percent above all others, but the clipped plots appeared to hold no consistent advantage over those which were not clipped. The fact that a nearly pure stand of muhly supplanted the original fescue association on the two plots which were denuded but not weeded has suggested that these two plots, on account of the rela-

FIG. 7. *A,* Undisturbed grass plot, nearly pure stand of Arizona fescue with a few plants of thistle. *B,* Plots before fall clipping, 1937. Left of path, 2-inch clipping plot, composition muhly, beardless bunch, and many forbs including vetch, yarrow, and geranium. Right of path, 6-inch clipping plot, composition same as above with the addition of a few plants of Arizona fescue. *C,* Same plots after fall clipping, 1937.



A

B

FIG. 8. Plots inside rodent exclosure, 1937 sowing. *A*, General view in 1938, looking west. Designation of plots in the order of Table 6, beginning with Plot 1, ''denuded-weeded'' on right side of path, and Plot 5 ''natural'' (dense grass) on left side of path. White sticks mark pine seedlings. *B*, Looking south at west end. Right, Plot 4, ''clipped to 4 inches'' and Plot 8 ''denuded-weeded.'' Left, Plot 3 ''denuded-not weeded'' (dense growth of 6-weeks grass), and Plot 7 ''clipped to 4 inches.''

tively low early-summer activity of muhly, might offer better soil moisture conditions than the fescue plots. Such, however, was not the case in 1941, the only year in which a comparison was made after full recovery of the muhly. This finding is not regarded as conclusive because muhly made more growth than usual in the early summer of 1941.

Seed spots sown in 1937 on an area adjoining this series of plots were a complete success (Fig. 10*A*). In all of these spots the grass was removed from a space about 3 feet in diameter and kept out the first 2 years. The seedlings, now in their 5th year, are from 9 to 15 inches tall and comparable to those on the denuded-weeded plots previously described. Seed spots in places where deep litter has killed out herbaceous vegetation have given similar results (Fig. 10B).

1938 SEEDING EXPERIMENT

The 1937 seeding was replicated in all essential details in 1938. The summer rains were less contin-

uous in 1938 than in 1937, with the result that germination was irregular and generally incomplete; nevertheless, substantial numbers of seedlings appeared in most of the plots. In this instance all the denuded plots, whether weeded or not, were superior to the grass plots in point of germination. But 1939 experienced one of the driest April-July periods on record, and 1940 the driest July on record. Both of these droughts took a heavy toll not only in outright mortality but also in retarding development. Although the late summer and fall of both 1939 and 1940 brought heavy rains, the weakened seedlings failed to respond. Ground heaving during the extremely wet winter of 1940-41 made the loss almost complete. One of the denuded not-weeded plots (Plot 13) proved an exception to the rule with 18 hills surviving on May 8, 1941. No explanation can be offered, except that frost heaving was less severe on this plot than on some others. Muhly forms a sparse stand—noticeably less dense than on the companion plot.

The fact that summer mortality was high on denuded-weeded as well as grassy plots indicates that in extreme drought elimination of competition may not be an adequate safeguard. Soil moisture determinations in July of 1939 and 1940 would have been enlightening. A reasonable conjecture is that the moisture content fell below or very near the wilting point on denuded as well as on grassy plots.

TABLE 7. Survival of pine seedlings grown from seed under different treatments of herbaceous vegetation. 1938 seeding.

Plot No.	Treatment	Number of hills on different dates				
		Oct. 1938	Aug. 1939	May 1940	May 1941	Sept. 1941
9	Denuded—not weeded	46	15	7	2	0
10	Natural	6	1	0	0	0
11	Clipped to 4 inches	8	2	0	0	0
12	Denuded—weeded	38	13	4	2	1
13	Denuded—not weeded	56	23	19	18	18
14	Clipped to 4 inches	20	1	1	1	1
15	Natural	7	1	0	0	0
16	Denuded—weeded	62	28	25	1	0

PLANTING

In 1938, 3-year-old nursery-grown ponderosa pines were planted in denuded and grassy spots. Four plants were set in a space 6 feet square and the squares were located randomly. The results in Table 8 show a decisive margin in favor of the denuded plots. In this case, the effect of grass is attributed entirely to root competition since the planted trees, 4 inches or more in height, were tall enough to evade intense shading. Although the tree roots were for the most part long enough to reach below the zone of most itense grass-root activity, the laterals evidently encountered severe competition from grass roots.

TABLE 8. Survival of 3-year-old nursery-grown stock planted May 2, 1938, in natural grass cover and on denuded spots.

Grade of stock	Number planted	Survival	
		August 1	October 28
		Percent	*Percent*
Planted in natural grass cover			
First	58	44.7	40.0
Second	58	11.4	8.6
Planted on denuded spots			
First	56	94.8	91.1
Second	56	63.8	57.2

In the two grades of stock, root development was the main criterion. On the average, first-grade plants had roots about 10 inches long, well branched and well supplied with fine rootlets; second-grade plants had shorter roots with fewer and weaker laterals and presenting only about one-half the absorbing area of the roots in grade 1. The superiority of grade 1 plants is decisive in both grassy and denuded spots; but it is most striking in the grassy spots, indicating that here root competition is most keen.

Follow-up records are not presented in this instance because deer browsing has all but destroyed the plantation. The surviving plants are nearly all in denuded squares, where occasional stems are over 2 feet tall. As a result of this and similar tests in 1935, 1936, and 1937, removal of competing vegetation around planted trees or "seed spots" has been adopted as standard practice in the Fort Valley Experimental Forest.

TRANSPIRATION

In view of the generally accepted experience that transpiration is directly related to leaf area, the failure of clipping to show a clear-cut response in soil moisture may call for explanation. Measurements of water loss by transpiration of potted plants plus evaporation were made in 1935 and 1936 with clipped and unclipped grass, forbs, and control pots of bare soil. Seven clumps of Arizona fescue were dug with a ball of earth attached to the roots and fitted into 5-gallon cans. The grass was removed from three clumps by cutting below the root collar; in two of these cans the soil was kept bare by weeding, while in one a volunteer stand of forbs or "weeds" was permitted to grow. After heavy watering had raised the water content to the calculated capacity of the soil, the cans were allowed a period of adjustment; then, when vigorous growth was in progress, two of the grass clumps were clipped to a height of 2 inches and the other two allowed to grow undisturbed. Because of the large size of the grass clumps, sealing against evaporation and rain was not considered feasible. Moreover, since grass covered the soil sur-

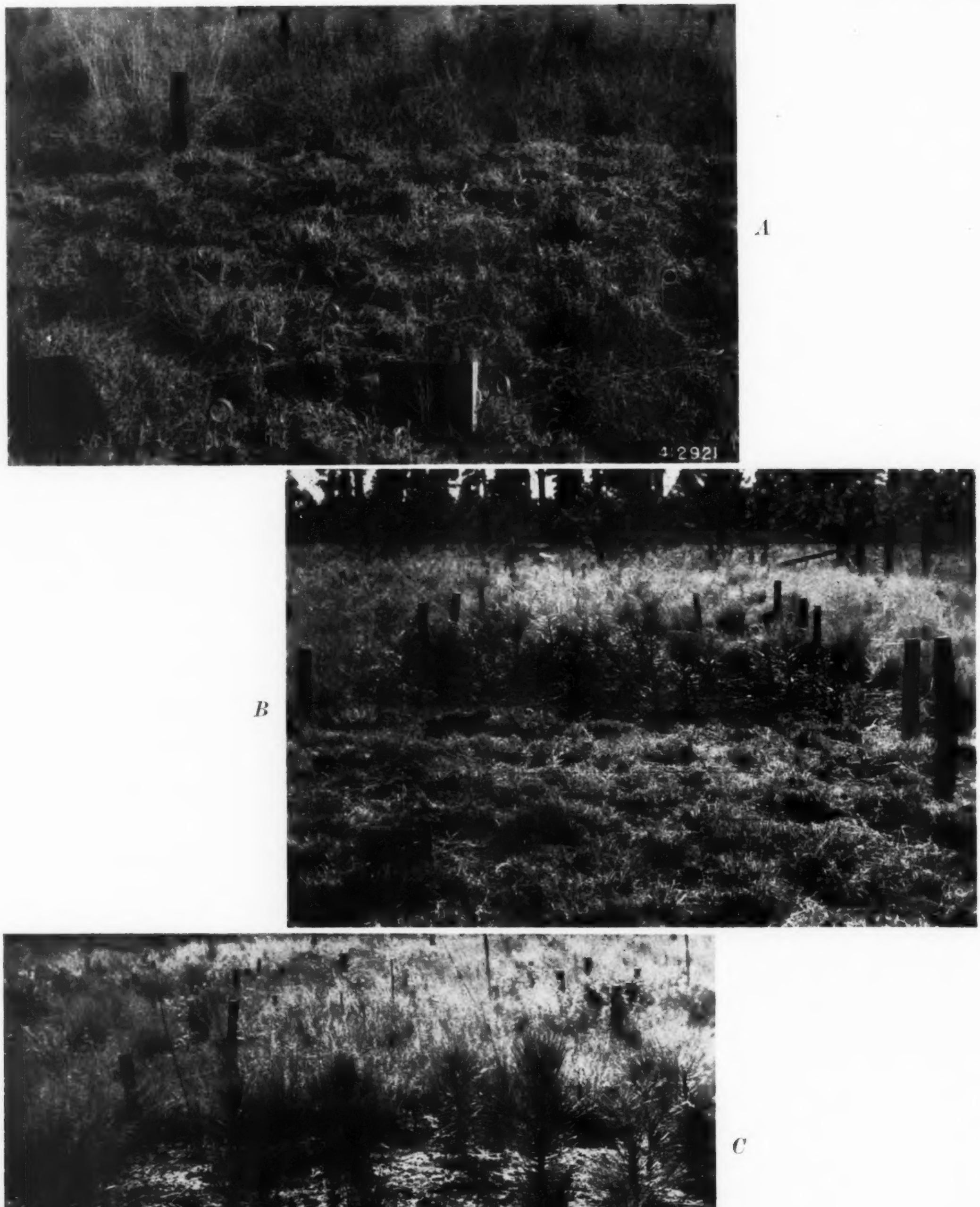


FIGURE 9

1937 seeding plots photographed in 1941. The plot numbers following refer to Table 6.
A, Foreground, Plot 4 (clipped to 4 inches) and beyond it Plot 3 (denuded-not weeded) now has dense stand

D

E

FIGURE 9 (continued)

of muhly. *B*, Foreground, Plot 4 and beyond Plot 8 (denuded-weeded). *C*, Foreground, Plot 8 and beyond Plot 7 (before clipping). *D*, Foreground, Plot 5 (dense grass with lupine) and beyond Plot 1 (denuded-weeded). *E*, Foreground, Plot 1 (denuded-weeded) and beyond Plot 2 (sparse grass with lupine).

face almost completely, evaporation in the grass cans was reduced to a low quantity.

During a rainless period of 17 days from June 18 to July 5, 1935, average daily water losses were: bare soil 141 grams, weeds 405 grams, clipped grass 249 grams, unclipped grass 339 grams.

In 1936, during a rainless period of 17 days from June 2 to June 19, average daily losses from the same cans were: bare soil 82 grams, weeds 144 grams, clipped grass 114 grams, unclipped grass 210 grams. The consistently lower water losses in 1936 than in 1935 are attributed to lower maximum temperatures and less advanced growth in the 1936 period which was nearly 20 days earlier than the 1935 period. Although this simple test is lacking in refinement as a measure of transpiration in relation to leaf surface, it is adequate for the purpose intended.

The relatively low water loss from the cans of bare soil as compared with cans containing grass or weeds is in accord with the widely accepted finding that plants may extract more water from a soil than is lost by direct evaporation. The dry air of the Southwest removes water from superficial layers of bare soil very rapidly, but after evaporation has dried the top layer to a depth of several inches, this layer acts as a blanket to retard evaporation from lower depths. If plant roots extend into the moist substratum, they may remove water more rapidly from the entire soil mass than is possible through evaporation alone.

A

B

FIG. 10. Seed spots. *A*, Grass removed in space 3 feet in diameter. Seed sown in 1937, photo 1941. *B*. Seed sown in disintegrated brush pile, 1938; photo 1941.

Broad-leaved plants are capable of removing water quite as rapidly as grasses. Obviously, the density and character of the weed composition is a factor. In this case several species, both annuals and perennials, were represented, all coming from seeds or roots which happened to be in the soil.

Water loss in the cans containing clipped grass was consistently below the loss from unclipped grass. This was true of individual cans as well as when the results were averaged; and the relation held for current losses, shown by weighing at 3-day intervals, as well as for totals. Since the grass cans were almost

completely stocked with grass, weeds were not a disturbing factor.

Any comparison of clipped and unclipped grass with respect to water consumption under field conditions must recognize that leaf area of the grass is only one of several factors involved. Increased evaporation from the soil surface as a result of lightening the grass cover may compensate, in part, for any lowering of transpiration through the grass leaves. Another factor which tends to restore the balance is that clipping the grass encourages weed growth. Finally, even if it were demonstrated that, notwithstanding the above compensations, clipping results in a net decrease of water loss, the saving in soil moisture might be only temporary. In the course of a prolonged dry period, even the reduced leaf surface of the clipped plants might be capable of exhausting all available soil moisture. Putting it another way, lack of soil moisture might prevent the plants which have the larger leaf area from exerting their full transpiring capacity.

SHADE EFFECTS

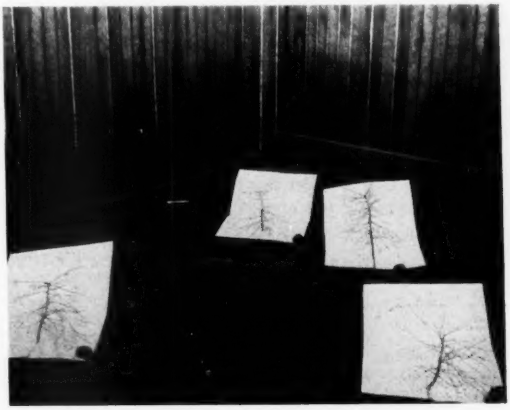
The interception of heat rays by a screen of plant leaves is easily demonstrated in the effect on soil temperature. Under tree crowns soil temperature at a depth of 6 inches is commonly 10° F. lower than in situations exposed to full sunlight. But this difference is most pronounced when the sky is clear or nearly so; on cloudy days temperatures are the same under tree crowns as in the open. A similar effect is reflected in evaporation from a moist surface.

Table 9 gives the results of measurements with Piche evaporimeters on 3 days in September 1937. The first day, September 21, was characterized as part cloudy with moderate wind; the other 2 days were clear with light wind. Wind was not much of a factor in any case because the site is surrounded by a dense stand of young trees, and therefore evaporation differences may be attributed almost entirely to insolation. The Piche evaporimeter lends itself well to measuring the effect of low plant cover because the flat evaporating disc can be placed underneath the foliage close to the ground.

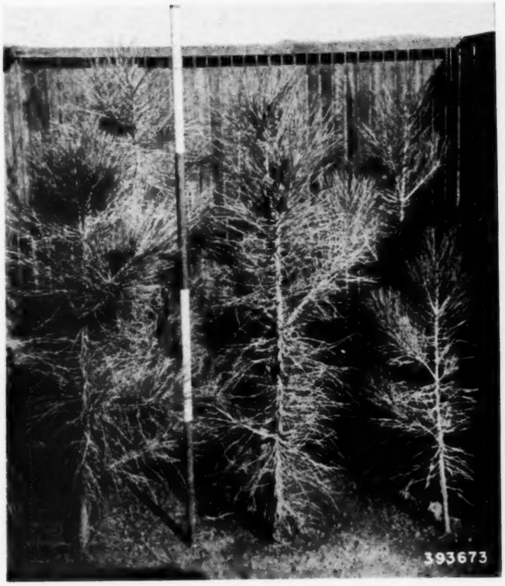
TABLE 9. Water loss from Piche evaporimeters placed 2 inches above the ground in different densities of grass cover.

Plot	Cover	Water loss, cubic centimeters		
		Sept. 21 10 a. - 4 p. Part cloudy	Sept. 24 10 a. - 6 p. Clear	Sept. 25 10 a. - 6 p. Clear
		cc	cc	cc
1...	Bare soil	14.0	15.6	22.3
2...	Grass, open stand	11.6	13.0	18.5
4...	Grass clipped to 4 in.	11.6	13.1	14.4
5...	Dense grass	10.2	8.7	13.4
5a..	Dense grass	....	....	12.6
8...	Bare soil	14.1	16.0	24.2

Although the shade of grass and other living vegetation retards evaporation from the soil surface and presumably also lowers transpiration in pine seedlings, it does not follow that the shade effect is wholly beneficial. An experiment begun in 1929 in which ponderosa pine seedlings were grown under artificial shade, with root competition from other vegetation eliminated, has demonstrated that seedlings in half shade assume a form so slender that the stems bend over, and that when insolation is reduced to about 15 percent of full sunlight the seedlings become dwarfed and finally die (Fig. 11).



A



B

FIG. 11. Effect of shade. Two-year-old pine seedlings planted in 1934 within lath screen, lath spaced to admit 15 percent of full sunlight. Photos in 1940. *A*, Screened overhead as well as on sides. Out of 10 seedlings planted only 4 survive. *B*, Screened only on sides, open overhead. Seedlings were identical with those in *A* when planted.

It has been pointed out in a previous paper that shading involves not only "light" in the technical sense but also heat and other forms of energy including the short wave lengths which are said to give rigidity to plant stems. Because high temperatures induce drought it is customary to think of heat as harmful; but there is much evidence that the highest temperatures that occur in the ponderosa pine type of this region are none too high for ponderosa pine and that the species does not function effectively if the normal heat supply is materially reduced. A small pine seedling under a clump of tall grass is subjected to the same influence as the disc of a Piche evaporimeter. The seedling, like the evaporimeter, saves water but the seedling also is deprived of solar energy for photosynthesis and other functions necessary for growth.

Seedlings which ultimately survive in dense stands of unclipped Arizona fescue are almost invariably in fair-sized openings between grass tufts or in the edge of a clump where they have access to direct sunlight. They remain subnormal in size for many years. Soil moisture has been found rather lower in these situations than in the shade of the grass, which is to be expected because root action is no less and evaporation is higher in the open spots. A somewhat similar situation is found in the edges of the denuded plots adjacent to grass plots or grassy paths. Survival is poorer and the seedlings are noticeably smaller than those well within the denuded plots. Within the two "denuded-weeded" plots of the 1937 series, the seedlings on a strip 1 foot wide along the border were all below 6 inches tall, whereas those inside of this border strip were commonly above 9 inches and as much as 16 inches tall. In these instances root competition is thought to be the sole retarding factor.

CONCLUSIONS

Experimental and observational data gathered over a period of more than 20 years confirm the findings elsewhere in this country and in Europe that dominance of herbaceous vegetation retards and may prevent regeneration of forest trees. Since pine seedlings were found in this study to grow well after removal of the grass on sites where failure was previously experienced, it is fair to conclude that the presence of grass rather than an inherent soil condition was primarily responsible for the failure.

Soil moisture seems to play the leading role. The critical factor is not so much surface moisture for germination as moisture below the surface, required to sustain life and growth after germination. Grasses and other herbaceous plants are able to appropriate the moisture in the upper 9 inches of soil at the expense of young pine seedlings. If, however, the pine is able to survive several years, its roots may eventually extend below the dense network of grass roots; the pine in that case also develops strong superficial roots and gradually gains the upper hand. The small seedlings in Figure 12 illustrate the effect of competition upon both stem and root development; the roots were found literally embedded in a maze of grass roots. Figure 5 illustrates 12-year seedlings which have emerged from suppression.

FIG. 12. The large seedling is an average specimen from denuded-weeded Plot 1 (Table 6). The small seedlings are samples of the few survivors in the grass of Plots 2 and 5. Note that roots as well as tops of the small seedlings are underdeveloped; they are full length as found enmeshed in a network of grass roots. The tops were partially covered by grass. Both large and small seedlings are 5 years old.

Although the influence of soil moisture has been clearly demonstrated, this does not preclude the possibility of other influences due to grass competition. Insolation may be an important factor. Many small seedlings are completely covered by mats of dead grass; others are in continuous shade under the dense foliage of Arizona fescue. Seedlings in the unclipped grass plots commonly show the characteristic symptoms of etiolation.

When the apparently conflicting evidence has been reduced to elementary terms, the confusion clarifies. The findings here presented point to certain guiding principles or, more correctly, to a confirmation of old silvicultural teachings. European silviculture stresses control of competing vegetation in both natural and artificial reforestation. It also stresses care of the soil by maintaining what is called "forest conditions."

Trees, like any other crop, respond to cultivation.

Old field pine in the South is a familiar example; examples may also be found in the Southwest. Extensive cultivation is not generally practical in a mountain country, on account of stony soils and topography subject to erosion, but the principles apply there as anywhere else. The old observation often cited by timbermen that tree regeneration is favored by scarification and denudation of the soil in the course of logging operations is scientifically sound; but these operations must be conducted with due regard for soil stability. Grazing can aid reforestation if directed toward silvicultural ends. Grazing confined to late summer and fall, and utilizing the forage in a degree comparable to that on the 2-, 4-, and 6-inch clipping plots in this study, has distinct silvicultural possibilities. Grazing to the extent of destroying grass cover over large areas is inadvisable as a general practice because of resultant soil deterioration.

In artificial reforestation, as already related, it has been found feasible to denude a spot about 3 feet in diameter for each planted tree or "seed spot." The spot must be weeded during 2 years after planting. This practice results in much higher survival and more rapid growth than if the young tree is subjected to competition with other vegetation during the first few years of its life. In fact, as shown in Table 8, even well-developed transplant stock is unable to compete successfully where grass has possession of the soil. It is often practical to take advantage of localized breaks in the grass cover, such as old roads, log landings, decayed brush piles, bare spaces around stumps or decayed logs, and areas covered by leaf litter and logging debris.

The foregoing measures apply mainly to lands on which the forest has suffered from past misuse, through overcutting, overgrazing, and fire. Usually it is only under these circumstances that pine regeneration presents a problem. Good silviculture encourages nature to bring about automatically favorable conditions which, under mismanagement, can be obtained only through artificial measures. In a well-managed forest, young trees start in small openings between groups of older trees; a mat of leaf litter keeps the soil mellow and promotes infiltration of water; openings in the crown canopy are seldom large enough to permit grasses to assume dominance. Ponderosa pine, though light-demanding, is less so than Arizona fescue, which thrives only in relatively large openings such as occur mainly after heavy cutting. Pine seedlings will endure side shade if they have access to direct sunlight from overhead; in fact, they develop the best timber form under these conditions. In a well-managed pine forest on the Colorado Plateau, Arizona fescue will eventually give way to the more shade-tolerant muhly, more desirable silviculturally and more palatable to livestock than is Arizona fescue.

Once the forest has regained dominance, the best cure for grass competition is forest management which does not permit grasses to assume a dominating position. Management must begin in the virgin stand by encouraging advance reproduction in open spaces before they are enlarged by cutting. Unlike some forest trees, ponderosa pine is a climax species which is capable of directly succeeding itself. Given the active co-operation of man, the ponderosa pine forests of the Southwest will remain as pure stands of ponderosa pine and they can be made to improve rather than decline with use.

SUMMARY

Grass is the prevailing type of herbaceous vegetation or "ground cover" in the ponderosa pine forests of the Southwest. In general, grasses predominate on the heavier soils and shrubs on the lighter soils.

A pronounced midsummer rainy period in the Southwest favors grass vegetation whose intensive superficial root system is well adapted for utilization of the water from summer showers.

Trees, like shrubs, prefer porous soils favorable to deep root penetration. Where winter precipitation is sufficient to saturate the soil to a depth of several feet, old trees are relatively independent of summer showers.

Pine seedlings require moisture in the superficial soil layers during the first few years of their life, or until they have developed a deep root system. During this period grass competition places them at a serious disadvantage.

The intensity of root competition varies according to the growth habits of different grasses. Arizona fescue, a tall bunchgrass, is the most aggressive competitor because it grows during May and June when precipitation is at a minimum; other bunchgrasses, such as mountain muhly and beardless bunch and the short grass, blue grama, compete less because they remain almost dormant during the early summer dry period.

The foregoing relationships, observed over a long period of years, have been checked experimentally since 1928 on plots artificially seeded to pine, protected against rodents, and otherwise treated uniformly with respect to all factors except herbaceous vegetation.

On some plots grass was permitted to grow undisturbed; on others it was clipped to various heights; some were denuded by "scalping" the soil to a depth of about 2 inches and kept clean by weeding; others were scalped but not weeded, allowing vegetation to return at will.

The first installation in 1928 was repeated on different sites in 1929, 1937, and 1938. Excellent germination took place on all plots in 1929 and 1937, and both of these sets of plots are thought to afford a reliable test of the influence of grass.

In both the 1929 and the 1937 series, by far the best survival and growth were obtained on plots which were denuded and kept continually free of all competing vegetation; results were poorest in undisturbed grass and intermediate in clipped grass. Denuding without subsequent weeding gave variable results, generally most comparable to clipping.

Soil moisture is thought to account more than any other factor for the difference in behavior under different treatments. During wet periods the soil moisture content was rather higher on the plots densely covered by grass than on the denuded plots, but during drought periods the relation was reversed.

Clipping did not appreciably influence soil moisture. Although clipped grass was found in a separate test to use less water than unclipped grass, this saving is apparently offset under field conditions by increased evaporation and by increased activity of forbs on clipped plots.

Light appears to be an important secondary factor favoring development on denuded and closely clipped plots. Young seedlings in tall grass exhibited the familiar characteristics of etiolation. Ultimate survival on unclipped grass plots was invariably in open spaces a foot or more in diameter.

Under a program of clipping twice annually through 10 years, Arizona fescue was replaced almost completely by mountain muhly, beardless bunch, and forbs when clipped to 2 inches, but less completely when clipped to 6 inches. On plots denuded once and not subsequently disturbed, muhly by sprouting from the roots recovered completely whereas very little fescue returned.

Managed grazing can aid pine reproduction materially; but grazing to the point of denudation is not generally advisable because it results in the browsing of seedlings and the packing of soil in valleys and erosion on slopes.

Cut-over lands on which Arizona fescue has become dominant may require artificial measures to aid pine reproduction; but pine stands in good silvicultural condition when logged the first time can be managed in such manner that grass will not introduce a reproduction problem.

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